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Growing Up Tamarin: Morphology, Reproduction, and Population Demography of Sympatric Free-ranging Saguinus fuscicollis and S. imperator

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by

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ABSTRACT OF THE DISSERTATION

Growing Up Tamarin: Morphology, reproduction, and population demography of sympatric free-ranging *Saguinus fuscicollis* and *S. imperator*

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The Callitrichidae are family of small New World primates with a suite of distinctive morphological and behavioral adaptations that set them apart from other primates. Of primary interest is their reproductive system that includes compulsive twinning (>80% of births) and cooperative care of offspring by individuals other than biological parents (termed alloparenting). Further, hematopoietic tissues in callitrichids display signals of both self and sibling DNA, due to an exchange of stem cells early in gestation that renders twin callitrichids as cellular mosaics of each other. This phenomenon is known as genetic chimerism, which increases genetic relatedness between individuals and is likely maintained by cooperative breeding systems. The Callitrichidae are thought to be phyletic dwarfs that exhibit habitual twinning as a derived feature, and accompanied by their tolerance for genetic chimerism, are an important clade to study the evolution of primate reproductive system that has adapted to increased reproductive outputs. They are suspected to be highly polyandrous, where additional male mates assist in the care of a dominant female's reproduction, and subdominant females are reproductively suppressed so that all efforts at alloparenting are directed towards offsetting the high energetic costs of raising a single set of infants of the dominant female. To better understand the evolutionary advantages of this system of reproduction, it is important to document group structure and membership, as well as individual dispersal, reproductive success, and the development of offspring across callitrichid species.

The goal of the present study was to examine group structure, reproductive success and individual growth and development to assess two sympatric *Saguinus* spp. These data are evaluated in light of the reproductive system proposed for these callitrichids – strict polyandry, cooperative breeding, reproductive suppression, and single reproducing females – in the context of future genetic studies. As such, I attempted to achieve three specific goals – first, an examination of morphological variation between two sympatric callitrichid species; second, an evaluation of age and reproductive status per individual; and third, a

comparison of group compositions, mating systems and dispersal patterns of both species to the expected callitrichid reproductive pattern.

I monitored two sympatric species of callitrichids in southeastern Perú at a field site named CICRA over the course of three years – 57 animals in 7 groups of saddleback tamarins (*Saguinus fuscicollis*), and 36 animals in 6 groups of emperor tamarins (*S. imperator*). I used an annual capture and release protocol to individually identify all animals, and recorded 19 measures of morphology and dental condition for all subjects. Behavioral data on mating, dispersal, and monthly group-compositions were also obtained, with an emphasis on one focal group per species. I used dental morphology to estimate age for animals < 1 y old (via dental eruption timings) and assigned age-categories for animals > 1 y old via molar occlusal wear. I assessed changes in morphology with age and sex for both species, comparing these measures using Mann-Whitney U tests ($\alpha = 0.05$), and used reproductive morphology to assign breeding status to adults, identifying primary, secondary, and non-breeders for both sexes. I then identified the predominant mating systems based on the number and sex of breeding adults in a group for both species.

I present here a modified trapping protocol for capturing callitrichids with a dual-step anesthetization protocol that increases animal safety and preserves habituation, resulting in 100% recapture rates. Age-structures predicted by dental wear did not differ significantly between species, or between the sexes for each species. Further sampling of younger adults in the study population is required to conduct population viability analyses. Adult *Saguinus imperator* (533 ± SD 79 g females vs. 495 ± SD 45 g males) are significantly heavier than adult *S. fuscicollis* (395 ± SD 30 g females vs. 385 ± SD 35 g males), with and without pooled sexes. Among *S. imperator*, significantly thicker limbs and not an overall increase in body size account for this increased weight. No sexual dimorphism was recorded for either species, save in upper arm lengths among *S. fuscicollis* (slightly longer in

females) and waist circumferences in *S. imperator* (slightly larger in females, but unrelated to pregnancy).

There are no significant differences between the species in the size of their genitalia or scent glands, despite differing markedly in their physical appearance (i.e shape and pigmentation). No significant effect of month was found on testicular volume, vulvar indices or suprapubic gland areas (Kruskal-Wallis rank sum test, $p \geq 0.05$). Suprapubic scent gland areas are significantly higher among females than males for both species (e.g. in *S. fuscicollis*, gland area =267.5± 143 mm for females and 117.1±72.4 mm for males). Vulvar indices explain *ca*. 70% of variation in suprapubic gland area for females of both *S. fuscicollis* ($R^2 = 0.70$, $P \leq 0.001$) and *S. imperator* ($R^2 = 0.76$, $P \leq 0.001$), while testicular volumes explain suprapubic gland areas only among male *S. fuscicollis* ($R^2 = 0.63$, $P \leq 0.001$). Male *S. imperator* have undifferentiated glands in general, unrelated to age or breeding status. While vulvar indices initially appear to grow faster than testicular volumes in both species, by 1.5 years of age, males have fully developed genitalia while females still appear underdeveloped. Morphological scores assigned to genitalia and glands encompass their range of variation, and can be used to distinguish infants from adults, but not other age classes (scores are too variable among adults). This highlights the singular importance of evaluating age based on dentition and not reproductive measures for either species, as reproductive suppression can be misleading and cause animals to appear younger than they actually are.

Twinning and strong birth seasonality were observed in both species, with overlapping birth peaks influenced by the environment occurring during the wet season (*ca*. September to March). Primary breeding males had higher testicular volumes than secondary breeding males (44-287% higher in *S. fuscicollis* and 24-80% higher in *S. imperator*), indicating possible subtle reproductive suppression of males. Secondary

breeding females had lower vulvar indices and suprapubic scent gland areas than primary breeding females, and required 2-3 y to acquire secondary breeding status compared to 1 y for males. This is evidence of reproductive suppression of females, but it was not as strict as expected, as evidenced by multiple instances of two primary breeding females reproducing in the same group. Groups of both species display group compositions that encompass multiple adults of both sexes. Their mating systems, however, tend to be polyandrous among *S. imperator* and polygynandrous among *S. fuscicollis*. Overall, no sex ratio biases were observed at the level of the population or group; although operational sex ratios indicate that male *S. imperator* have to share their mate with more males than do male *S. fuscicollis*.

Immigration events are significantly less common than emigration events, with breeding females having extended tenures in both species. Cold fronts known as *friajes* create breeding vacancies among groups, which were filled by individuals from outside the group. Overall, *Saguinus imperator* appears to be more similar in terms infant survivorship and mean reproductive output to both the CICRA and Cocha Cashu populations of *S. fuscicollis*, than it is to *S. mystax* at other long-term study sites. However, *S. fuscicollis* has a slightly higher reproductive output likely achieved by its polygynandrous mating system, maintained by reduced reproductive suppression, in which multiple females breed successfully in a group. Therefore, it does not appear that groups of these two species conform to one, invariable mating system or group structure. It is likely that this variability may apply to other callitrichid species as well. There appear to be more ways than one to be a successful callitrichid. Further years of study, including an investigation of endocrine profiles, genetic population structure, feeding ecology, parasitism and genetic chimerism are also underway at this site, and will lend further insight into the range of variation among callitrichid reproductive systems in the wild.

Does a creature have to be of direct material use to mankind in order to exist? By and large, by asking the question "what use is it?" you are asking the animal to justify its existence ***without having justified your own.***

–– Gerald Durrell, Two in the Bush, 1966

Chapter I: General Introduction and Study Outline

I. 1: Introduction

Cooperative breeding systems, in which group members other than biological parents help raise offspring, are present among a diversity of taxa, including eusocial insects, birds (scrub jays, acorn woodpeckers), and mammals (naked mole rats, wolves, sperm whales) and primates (marmosets and tamarins) (Bergmüller et al. 2007; Clutton-Brock 2002; Hrdy 2007). Cooperative polyandry is a term used to describe groups in which two or more males mate with a single female and cooperate in raising her offspring, and it was first applied to the Galapagos hawk (*Buteo galapagoensis*) on Santiago Island in Ecuador (Faaborg et al. 1980). Multiple paternity of chicks in this species, and increased lifespans from membership in stable groups with established territories, compensate for males having to share mating opportunities (Faaborg et al. 1995). Cooperative breeding can be sustained by both polyandrous and monogamous mating systems, with different strategies for securing offspring survival displayed across several cooperatively polyandrous avian species (cf Goldizen 1987b). The Callitrichidae, a family of diminutive New World primates, have long been viewed as a classic example of a cooperative breeder, exhibiting polyandrous and monogamous mating strategies in the wild (Epple 1975; Goldizen 1988; Goldizen 1987a; Sussman & Garber 1987; Sussman & Kinzey 1984; Terborgh & Goldizen 1985).

A variety of factors are thought to characterize and facilitate cooperative breeding in the Callitrichidae, including habitual twinning and polyandrous mating systems (Garber 1997). However, for each generalization developed about their mating system and infant care patterns, there exists a corresponding exception, typically emerging from wild studies of callitrichids. Originally, callitrichids were considered monogamous breeders, with nonbreeding helpers that assisted in infant alloparenting; this interpretation of callitrichids initially arose from a reliance on studies of captive breeding colonies of callitrichids (Savage & Baker 1996). Later, as more

wild studies were conducted on these primates, the flexibility in their mating systems was revealed (Goldizen 1987a). Nevertheless, only a handful of studies have attempted to observe callitrichids in the wild for long enough to cover the upper ranges of their expected lifespans, and therefore, the majority of long-term data on callitrichid breeding come from captive colonies of a few species (Dietz et al. 1994; Ferrari & Digby 1996; Garber & Teaford 1986a; Garber & Teaford 1986b; Heymann 1990a; Savage et al. 1997; Terborgh & Goldizen 1985). Although several specific factors are credited with successfully maintaining cooperative breeding systems, such as polyandry, reproductive suppression, and delayed breeding, there is large variability in almost all of these characteristics, both within and between species. This seems to suggest that there are, in fact, many ways in which a successful system of cooperative breeding could be maintained.

It is often only feasible for a researcher to study social systems and reproduction in a single species of callitrichid in the wild. This results, subsequently, in methodological variation that renders data between sites and studies inadequate for direct comparison. However, in wild populations of sympatric callitrichid species, there remains an opportunity to conduct a natural experiment on two or more species within similar environments. In this context, how do interspecific differences in group composition, development and morphology correlate with cooperative breeding in callitrichid species? In the present study, I examine two sympatric species of callitrichids, the saddle back tamarin (*Saguinus fuscicollis*) and the emperor tamarin (*Saguinus imperator*), within the same environment and utilizing a single approach, to determine the extent to which anatomical and behavioral correlates of cooperative breeding relate to group structure. In this way, characteristics that are necessarily constrained by cooperative breeding in tamarins generally may be distinguished from those that can be more flexible. Specifically, I will focus on the reproductive maturation of young individuals, the securing of breeding opportunities, and the factors that determine an individual's ontogenetic

trajectory and reproductive output in two sympatric, cooperatively breeding species of callitrichid.

I. 2: Studies on Cooperative Breeding in Callitrichids

The archetypal cooperatively breeding callitrichid group is thought to contain a single dominant and reproductively active female, her twin offspring, and a handful of individuals, typically her mates and older juvenile offspring, that assist in raising the infants (Sussman & Kinzey 1984). Data from wild studies confirm that callitrichids cannot be subject to facile categorization due to the large variability observed in their reproductive behaviors (Terborgh & Goldizen 1985). Therefore, to better understand cooperative breeding among callitrichids, it is essential to describe variation observed between and within species. I will consider here the factors that are commonly viewed as characteristic of cooperative breeding in callitrichids, with an emphasis on the genus *Saguinus*.

A few long-term studies have been conducted on the genus *Saguinus*, including the study of *S. fuscicollis* and *S. imperator* at Cocha Cashu in Peru (Goldizen et al. 1996; Terborgh 1983; Terborgh & Goldizen 1985), *S. oedipus* in Colombia (Savage 2011) and Panama (Dawson 1978; Neyman 1977), *S. mystax* at Padre Isla in Peru (Garber et al. 1984), *S. labiatus* at San Sebastian in Bolivia (Porter 2004; Suárez 2007) and the Fazenda Experimental Catuaba in Acre, Brazil (Garber & Leigh 2001; Rehg 2006), and *S. fuscicollis* and *S. mystax* the Estación Biológica Quebrada Blanco (EBQB) (Garber & Teaford 1986b; Heymann 1990a; Huck et al. 2005a).

Table I. 1: Site comparisons for long-term studies of Saguinus spp. in Perú

Study Features	Cocha Cashu *Saguinus fuscicollis*	Padre Isla *Saguinus mystax*	EBQB *Saguinus mystax*	CICRA *S. fuscicollis*	CICRA *S. imperator*
Study Years	1979-1992	June – Nov. 1990	1999-2003 main year 2001	2009-2012	
Duration	13 years	~ 1 year	5 years	3 years	
Total # of groups	4 to 7 groups	16 groups	8 groups	7 groups	6 groups
Focal groups	All	2	2 groups	1 group	
Sympatric species	*S. imperator*	None present	*S. fuscicollis*	*S. imperator*	*S. fuscicollis*
Multiple species used	Not in the major study	N/A	(Heymann 1990a)	√	√
Behavior	(Goldizen 1987b)	(Garber et al. 1984; Heymann 1990b)	(Herrera & Heymann 2004; Heymann 1996; Löttker et al. 2007)	√	√
Capture	(Goldizen et al. 1996; Terborgh & Goldizen 1985)	(Garber et al. 1993)	(Garber et al. 1996) early, but not with later studies	√	√
Morphology		(Garber et al. 1996)	(Garber et al. 1996)	√	√
Dentition		(Tornow et al. 2006)		√	√
Endocrinology			(Huck et al. 2005b; Huck et al. 2004b; Löttker et al. 2004b)	©	©
Parasitology			(Wenz et al. 2010)	©	©
Genetics			(Huck et al. 2005a; Huck et al. 2007)	©	©
Home range	(Terborgh 1983)	(Garber et al. 1984)	(Löttker et al. 2004a)	©	©
Scent marking		(Heymann 1998)	(Heymann 2001; Lledo-Ferrer et al. 2010; Lledo-Ferrer et al. 2011)	√	√
Feeding ecology		(Garber 1993)	(Garber 1993; Garber 1988; Garber 1986)	©	©
Vocalizations	(Windfelder 1997a)			©	©
Age-estimation	Based on morphology	Based on dentition	None	Based on dentition	

√ = Present; © = Collected but data not presented, pending analysis

However, not all of these studies have focused on reproductive characteristics, and so three main sites will be primary points of comparison: *S. fuscicollis* at Cocha Cashu (Goldizen et al. 1996; Terborgh 1983; Terborgh & Goldizen 1985), *S. mystax* at Padre Isla (Garber et al. 1996; Garber et al. 1993), and *S. mystax* at the Río Blanco (EBQB) (Garber & Teaford 1986b; Heymann 1990a; Huck et al. 2005a). The primary study features are compared in Table I. 1.

I. 2. 1: Twinning

Twinning in callitrichids was recognized early on in captive-housed common marmosets (*Callithrix jacchus*) through studies of placental development (Hampton & Hampton 1965a; Hampton & Hampton 1965b; Wislocki 1932). These studies established a pattern of double ovum twinning, since corpora lutea were observed in each ovary in > 40 cases of pregnancy (Wislocki 1932). In captivity, it was further observed that marmosets also gave birth to fraternal twin offspring > 80% of the time (Wislocki 1939). Studies have since indicated that callitrichids can produce from one to four offspring per litter, with strong indication that ovulation number varies with maternal nutrition and body mass (Tardif et al. 2003).

In captivity, triplets are the most commonly observed litter size among common marmosets (Tardif et al. 2003). In the wild, on the other hand, triplets are very rarely observed, with twins and singletons being more common - a likely indicator that resource limitation affects reproductive output. While some genera of callitrichids produce two litters a year in the wild, *Saguinus* and *Leontopithecus* typically breed only once a year (Bales et al. 2001; Goldizen 1987a). Studies reveal that *Saguinus* twins regularly in the wild, with a strong single breeding season coinciding with an abundance of fruit resources (Goldizen et al. 1988); however, the precise timing of the season itself may vary by species – August to March in *S. fuscicollis* at Cocha Cashu (Goldizen et al. 1988), March to June in *S. oedipus* in Colombia (Savage et al. 1997), and September to May in *S. mystax* at Río Blanco (Löttker et al. 2004b). At Padre Isla in Perú, birth were observed year round, but the majority occurred from June to October (Garber

et al. 1993). It is likely that site differences in weather or resource availability could affect breeding seasonality.

I. 2. 2: Breeding and Infant Care

Several factors indicate that rearing twins poses an acute strain on caregivers, including high neonate-to-maternal weight ratios (Goldizen 1987b), high energetic costs of infant lactation and transport (Tardif 1994), and weight loss in helper males (Achenbach & Snowdon 2002). It has been suggested that routine twinning has necessitated cooperative breeding (Tardif 1994), supported by evidence from wild studies that no single breeding pairs were observed to raise twin offspring, for example, in a 13-year study period among *S. fuscicollis* at Cocha Cashu in Peru (Goldizen & Terborgh 1989). Reproductive output, or the number of surviving young per group, was found to be three times as high in groups with three adult male helpers as opposed to those with a single male (Garber 1997), indicating the necessity for assistance to ensure offspring survival.

I. 2. 3: Reproductive Suppression

Among callitrichids, group composition is further characterized by the monopolization of breeding by a single dominant female in most cases. This can be achieved through physiological or behavioral suppression of other females within the group (Barrett et al. 1990; Savage et al. 1988). Female juvenile callitrichids are thought to exhibit delayed maturation within their natal groups, via hormonal and social suppression of reproduction (Ginther et al. 2002; Ziegler et al. 1987). Generalized stress does not appear to cause such delays in breeding, since higher cortisol levels are found in dominant and not subordinate females (Abbott et al. 1997). Although some form of delayed breeding has been observed in all callitrichid species, the mechanisms by which suppression is facilitated differ by genera, and between captive and wild studies. *Saguinus fuscicollis* is known to show delayed breeding of 2-4 years in both sexes (Goldizen et al. 1996), while *S. mystax* displays delayed breeding as well, with evidence of different schedules of

maturation even between twins (Huck et al. 2004b). However, a study of captive *S. oedipus* showed that young females (ages 20-28 mo) exhibit suppressed ovulation and low, acyclical levels of luteinizing hormone. Although evidence from the wild does support this outcome in some cases, young females were also observed to cycle, and even conceive, while in a natal group (Savage et al. 1997). Among wild *Saguinus mystax*, no differences between hormonal profiles of dominant and subordinate females were observed and data from captivity on this species are unavailable at this time (Löttker et al. 2004b).

A dominant female has other means to ensure that her offspring are the focus of all helpers' attention when they are born. There is evidence from wild callitrichids of harassment of younger pregnant females by the dominant breeding female, extending to some instances of infanticide (Lazaro-Perea et al. 2000; Smith et al. 2001). Studies have also noted that social suppression can play a role in delayed breeding, with subordinate females unable to initiate cycling until they encounter with an unrelated male (Saltzman et al. 2004), which is a feasible mechanism for inbreeding avoidance.

The reproductive suppression of natal males has also been detected among captive callitrichids, and is attributed primarily to the avoidance of mating with familiar females rather than hormonal suppression (Baker et al. 1999). Further, enlarged testicular volumes among breeding males have been observed in *Callitrhix jacchus* (Araújo et al. 2008) and *Saguinus mystax* (Garber et al. 1996) in the wild, suggesting the use of this measure to identify possible breeding males among groups in the wild.

Despite the evolution of these behaviors to assume single, dominant breeding status within a group, multiple breeding females have been observed in several species (Digby & Ferrari 1994; Saltzman et al. 2004), including four breeding females in a single group of *Callithrix flavus* (Hilário & Ferrari 2010). Most remarkably, cases of allo-nursing, or the nursing of infants that are not one's own, have been observed in the wild in several callitrichid

species (cf Smith et al. 2001). It appears that although physiological processes do underlie strict single-female breeding systems within a group particularly in captivity, variable conditions in the wild do not support the enforcement of restricted breeding in all cases.

I. 2. 4: Mating Systems

A large variety of mating systems have been observed among the Callitrichidae, and initial expectations of monogamy, largely due to their small size, relative lack of sexual dimorphism, and captive housing requirements, have been replaced with expectations of habitual polyandry, which themselves have been challenged by later work (Savage & Baker 1996). Groups have been suggested to contain largely unrelated adults in some species (Sussman & Kinzey 1984), while others have demonstrated stable extended families, where juveniles and helpers are largely offspring of the dominant female, do exist among callitrichids (Goldizen et al. 1996; Huck et al. 2007; Löttker et al. 2004a; Nievergelt et al. 2000). This is possibly the most flexible of all characteristics of a cooperatively breeding primate, with greater variation observed in *Saguinus* than in marmoset species. In a multiyear study at Cocha Cashu, in Peru, groups of *S. fuscicollis* exhibited monogamy, polyandry, polygyny and even polygynandry, where multiple males breed with multiple females and cooperatively raise their young, even within the same groups across the study period (Goldizen 1987a). This variation highlights the relevance of proximate factors, such as physiological characteristics of individuals, or stochasticity in demographic variables, that could affect the mate choices made by a group from one year to the next.

I. 2. 5: Dispersal

Dispersal in the wild is engaged in by both sexes among callitrichids, to varying degrees of success (Garber et al. 1993; Goldizen et al. 1996; Löttker et al. 2004a). It is difficult to confirm in the wild, as animals often disappear without conclusive evidence of dispersal or death. In *ca*. 40% of cases where both starting and ending groups were known at Cocha Cashu,

dispersing individuals moved into groups adjacent to their natal group (Goldizen et al. 1996). In the remaining cases, individuals dispersed two to three group territories away. Young females dispersed from natal groups slightly earlier (2.5 y) than did males (3.0 y), although these ages were not significantly different (Goldizen et al. 1996), and in all long-term studies of *Saguinus* spp., immigration events were less frequent than emigrations (Garber et al. 1993; Goldizen et al. 1996; Löttker et al. 2004a).

At least two males were observed to breed in their natal groups and share breeding opportunities with their fathers at Cocha Cashu. Several females were observed to copulate within their natal groups, and although some of these females later dispersed, others inherited the primary breeding positions within their groups after the disappearance of their mothers (Goldizen et al. 1996). Given how easily mating instances are missed in the wild, it is quite possible that these are underestimations of the true rate of natal breeders in this species. Male *Saguinus* spp. were observed to transfer routinely, sometimes returning to groups after absences of 3 months, and in other instances, transferring multiple times between groups (Goldizen et al. 1996; Löttker et al. 2004a). While some instances of dispersal by adult females of *Saguinus imperator* in Cocha Cashu were observed, many disappearances were not tracked successfully due to difficulty in trapping all the individuals within emperor tamarin groups at this site (Windfelder 1997b). The limited availability of breeding vacancies among groups for either sex, result in differing strategies between males and females for the acquisition of breeding opportunities.

I. 3: This Study

I conducted a three-year study on tamarins at the Centro de Investigación y Capacitación Río Los Amigos (CICRA) in the Madre de Dios of southeastern Peru. The two callitrichids included in the study are the saddleback tamarin (*Saguinus fuscicollis weddelli*) and the emperor tamarin (*Saguinus imperator imperator*), although the elusive *Callimico goeldii* is also

present (Watsa et al. 2012). While *Saguinus fuscicollis* has been the subject of numerous studies–including one of the longest running field studies on a callitrichid conducted at Cocha Cashu in southeastern Peru (Goldizen et al. 1996)–*S. imperator* has a much smaller distribution and is known from only a handful of studies (Aragón 2007; Bicca-Marques & Garber 2003; Knox 2011; Lopes & Rehg 2003; Terborgh 1983; Windfelder 1997b), including one detailed behavioral study on a captive population (Knox 2011). Of these long-term studies, those on *S. imperator* have largely concentrated on their feeding ecology and mixed species associations with other callitrichids (Terborgh 1983), and not on reproductive morphology or behavior.

The genus *Saguinus* has three major taxonomic subgroups - the hairy-faced tamarins, the mustached tamarins, and the black tamarin group (Hershkovitz 1977a). *Saguinus fuscicollis* belongs to the hairy-face tamarin group, while *S. imperator* is included in the mustached tamarin group, along with *S. mystax* and *S. labiatus* (Hershkovitz 1977a; Purvis 1995). *Saguinus fuscicollis* has *ca*.12 subspecies, while *S. imperator* has only two subspecies, *S. i. imperator* and *S. i. subgrisescens*. At CICRA, there is a sympatric population of *S. f. weddelli* and *S. i. subgrisescens*. In Chapter 2, I describe the primate community, climate and habitat surrounding this study population and the implications for conservation of research conducted at this site.

The current approach eliminates difficulties in comparing data from single species studied at different sites. Studies have repeatedly shown incongruences between wild and captive conditions that can influence animal physiology and behavior. For instance, single dominant females are the only ones to breed in most captive callitrichid populations, but in the wild, multiple females have been observed to carry pregnancies to term, and even raise offspring alongside other dominant females (Digby & Ferrari 1994; Goldizen et al. 1996; Löttker et al. 2004a; Smith et al. 2001). This is especially problematic in some species, such as *S. mystax,* that completely lack captive populations upon which to draw comparisons. Further,

environmental conditions can affect reproductive patterns, and studies of allopatric species in differing habitats cannot easily distinguish between environmental effects and intrinsic species-specific traits. In this study, both species share significant overlap in both the methods used and the duration of the study.

Studies of callitrichids produce information at the level of the group, when identities remain unknown due to morphological homogeneity between individuals. For more comprehensive and detailed information on individual breeding strategies and success, knowledge of individual identities is a must. This is typically achieved through a capture and release approach, which can be conducted safely and effectively, allowing for the placement of individual markers as well as radio telemeters on individuals (Aragón 2007; Dietz et al. 1994; Garber et al. 1996; Goldizen et al. 1996; Savage et al. 1993; Suárez 2007; Windfelder 1997a). Most of these studies have targeted single callitrichid species for capture and identification, with only a few exceptions. Both *S. fuscicollis* and *S. imperator* were studied for 13 years in the context of feeding ecology and mixed species associations at Cocha Cashu in the 1970s (Terborgh 1983), as well as more recently at the same site (Windfelder 1997b); nevertheless, difficulties related to the annual capture of *Saguinus imperator* have limited research on mating and breeding systems to *S. fuscicollis* alone at this site. At the Río Blanco site, an early capture of both *Saguinus mystax* and *S. fuscicollis* was conducted over 12 months (Garber & Teaford 1986b), but in subsequent years, animals were not monitored by capture (Huck et al. 2007; Huck et al. 2005a). The current study will compare multiple groups of both species, with identifiable individuals in each group, over the course of several years, for the first time in the wild.

Both species of tamarin are known to habitually twin, raise their infants cooperatively, and display polyspecific associations. We may expect a few possible outcomes when comparing *S. fuscicollis* at CICRA with those at Cocha Cashu (Table I.1). First, one could expect the

population of *S. fuscicollis* at CICRA to display similar dispersal or mating strategies to those at Cocha Cashu, given that both sites lie within the same continuous stretch of forest, are located near water bodies, and have combinations of floodplain and terraced forest; therefore, they should possess similar ecology. However, while Cocha Cashu has a full complement of large-bodied primates (Terborgh 1983; Terborgh et al. 1985), CICRA has low densities of howler, woolly, and spider monkeys (Pitman 2008), creating unexploited niches at CICRA that could affect the ecology of the callitrichids at this site. This lack of large-bodied primates could also have impacted predator densities, restricting them and thus relieving some predator pressure from the callitrichids at this site.

Since mating and breeding systems are not comprehensively studied in *S. imperator,* we could expect two possible outcomes for this species at this site. First, certain reproductive characteristics could be constrained by phylogenetic relatedness, in which case we would expect *S. imperator* at this site to display similar morphological and behavioral characteristics to other mustached tamarins, of which *S. mystax* is the best studied. Alternatively, other characteristics could be more susceptible to changes in ecology, and we would expect *S. imperator* to resemble *S. fuscicollis* at this site, as well as the population at Cocha Cashu.

I. 3. 1: Study Questions

In this context, I attempted to answer the following questions across both species at this site:

Q1. Do both species share similar age-structures at this site?

Age is a critical and yet extremely difficult characteristic to assess among wild primates. Often it requires long-term studies of known individuals through which, over sufficient time, the chronological age of every individual born in the population becomes known. In the absence of individual identities for the tamarins, I implemented a capture and release program for callitrichids at this site, for three years (2010-12) with saddleback tamarins and two years (2011-12) with emperor tamarins (Chapter III). This allowed me to place individual identification tags

on each animal and monitor morphological changes in dentition annually. Molar occlusal wear as well as eruption sequences determined from dental casts can be used in lieu of calibrated age schedules to identify age-classes for all individuals and possibly chronological age (accurate to the month) for individuals born during the study period (see Chapter IV). Utilizing life-history theory and transition tables I can then examine the age-structure of the population to set up a fundamental population viability assessment model.

Q2. How do somatometric and reproductive variables vary with sex and age among the callitrichid species at this site?

During capture, I recorded the size and appearance of external genitalia, scent glands, as well as the body mass and somatometric measurements across both species (see Chapters III and V). Reproductive suppression can affect the appearance of genitalia, which are frequently used to determine age, leading to routine underestimations of age among callitrichids. Since age will have been estimated based on dentition, I can examine how reproductive variables change over a lifespan, without that potential source of error. In the absence of hormone profiles for the study population, I developed a scoring key for the external genitalia of both species based on morphology, pigmentation, and size, in order to identify possible sexually mature individuals (Chapter V). The description of the range of variation in both the appearance and size of anatomical features associated with reproduction sets the stage for the evaluation of individual breeding behavior and status among groups.

Q3. Are reproductive variables (breeding status acquisition and determinations, breeding seasonality, twinning and mating behavior) similar between the two species at this site? How do they compare to other *Saguinus* spp. studied elsewhere?

Over the course of three years, the identity of breeding females and all instances of mating were recorded for focal groups of both species (Chapter VI). Thus, females that bred successfully and monopolized all mating opportunities could be distinguished from those that gave birth successfully but shared mating opportunities with other females in the group.

Alternatively, multiple breeding females within a group can be detected, which would confirm a lack of strict reproductive suppression in the wild (Löttker et al. 2004b). Individual reproductive output can be used to determine birth seasonality, infant mortality, and the contexts for possible reproductive suppression.

Q4. What strategies do males and females utilize to secure future breeding opportunities? In other words, when do they choose to stay in their natal groups vs. disperse to new groups?

The dispersal of individuals of both sexes is equally likely in *S. fuscicollis*, based on data from Cocha Cashu, although females tend to disperse from their natal groups slightly earlier (2.5 years) than do males (3.0 years) (Goldizen et al. 1996). A lack of breeding opportunities for females could motivate dispersal, which can account for the high mortality of females, *ca*. 2.5-4.5 years, and although the sex ratio is not significantly different from 1:1, there are more males than females in most years of the study (Goldizen et al. 1996). *Saguinus mystax* is known to have the highest mean number of males per group of any callitrichid species (Heymann 2000a). A spatio-genetic study of *S. mystax* has shown that both sexes also disperse in this species. Dispersal strategies of each species in these studies will be compared to those of *S. fuscicollis* and *S. imperator* at this site to determine if the same strategies for acquiring breeding status are utilized across sites (see Chapter VII).

Q5. Are there species differences in the extent to which groups adopt facultative polyandry as a mating system?

One of the main theories that favors the presence of male helpers in groups is that of facultative polyandry, where lone breeding pairs without nonfertile helpers are likely to recruit immigrants of both sexes into the group by offering them mating opportunities in return for assistance with infant care (Goldizen 1987b). Alternatively, if the only available helpers are related to the dominant breeding female, the mating system likely to be observed would be monogamy (Goldizen et al. 1996). An analysis of group compositions based on breeding status,

available breeding vacancies, and dispersal strategies will be conducted to determine if breeding pairs in this population (of either species) exhibit facultative polyandry or monogamy.

I. 4: Additional Research Goals

Additional datasets were accumulated during this study that can shed light on many aspects of reproductive behavior of the species in question. First, genetic material on all individuals has been acquired in this study, which will eventually allow paternity to be determined, but the results cannot be presented at this time due to restrictions on the export of genetic samples outside of Peru at this time. Second, scent-marking behavior was recorded for *S. fuscicollis* across 10 months, including the identity of the marker, as well as the type of scent-mark utilized. We are currently collecting a comparable dataset on *S. imperator* for further analysis. Endocrine profiles of these species are also being analyzed in conjunction with collaborators from the University of Missouri in St. Louis and the St. Louis Zoo.

In summation, a total of eleven groups of both species were captured once a year at a minimum to record data on dentition, development, general body condition, and genetics. By comparing a variety of behavioral and morphological features between these species, factors that appear to maintain cooperative breeding in callitrichids, such as delayed breeding, and the presence of male helpers and single dominant breeding females, can be examined for phylogenetic or ecological constraints. This study will contribute information on two new callitrichid populations to the overall discussion, including one species (*S. imperator*) that has never been the subject of a long-term study at this level of detail. The study has the added benefits of working with multiple sympatric species and a single research protocol for a controlled comparison. With these data, I will compare this study population to other studies of *S. fuscicollis* and *S. mystax* in the context of variables that are distinctive of cooperatively breeding callitrichids – delayed breeding in young individuals, single breeding females per

group, the presence of helpers with mating access to the breeding pair, and dispersal strategies for each sex.

Chapter II. Overview of the Study Site and Primate Community

II. 1: Study Site

The department of Madre de Dios of southeastern Perú holds the premier spot for tourism within Perú, driven largely by its easy access to tropical rainforest and its low population (O'Hare & Barrett 1999). It is adjacent to the state of Acre in Brazil and the department of Pando in Bolivia, and is bisected from Manu National Park in the west to Bolivia in the east by the Madre de Dios River. About 90 km west of Puerto Maldonado, the small but booming capital of the Department, the Madre de Dios River meets its tributary, the Los Amigos River. For its full course of 353 km, the Los Amigos River runs parallel to the great Andes mountain chain, forming the sixth largest watershed in the department (Pitman 2008).

The Los Amigos Conservation Concession (LACC) (12°30'–12°36'S and 70°02'–70°09'W) is nestled at the confluence of these two rivers, and extends west until the borders of the Manu National Park. It covers *ca.* 1400 km^2 of rainforest privately managed by the Associación para la Conservación de la Cuenca Amazonía (ACCA) (Fig. II. 1) (Tobler et al. 2008). The Centro de Investigación y Capacitación Río Los Amigos (CICRA) is ACCA's principal biological field station and is located in *ca.* 900 ha of once-logged tropical rainforest adjacent to the LACC.

The study population consists of two callitrichid species: *Saguinus fuscicollis* the saddle back tamarin, and *S. imperator,* the emperor tamarin. Focus groups occupied an area of *ca.* 4 km^2 surrounding CICRA (12°34'07"S, 70°05'57"W) (Fig. II. 2). Located in part on a terrace 50 m above the level of the Madre de Dios River (268 masl), CICRA is *ca.* 5.5 h upstream from Puerto Maldonado by boat. It boasts 61 km of trails, marked and geo-referenced every 25 m, of which half are regularly maintained.

Figure II. 1: A riparian map of the department of Madre de Dios (in grey) of southeast Perú. Two rivers, the Madre de Dios and Los Amigos are indicated in dark blue. Close to their confluence is the Centro de Investigación y Capacitación Río Los Amigos (CICRA) or the Los Amigos Biological Field Station (★). The Los Amigos Concession area is depicted in green. Geospatial information from http://atrium.andesamazon.org.

In addition, the site has a 900-m semi-permanent landing strip, and two smaller field stations, 3 km (CM1) and 21 km (CM2) upriver on the Los Amigos (Pitman 2008). The LACC itself has been described by R. Foster in more detail (within Janovec & Galvan 2003) and *ca*. 8% of all literature from the Madre de Dios department, including reports not formally published in the last 40 years, has emerged from this site (Pitman et al. 2009).

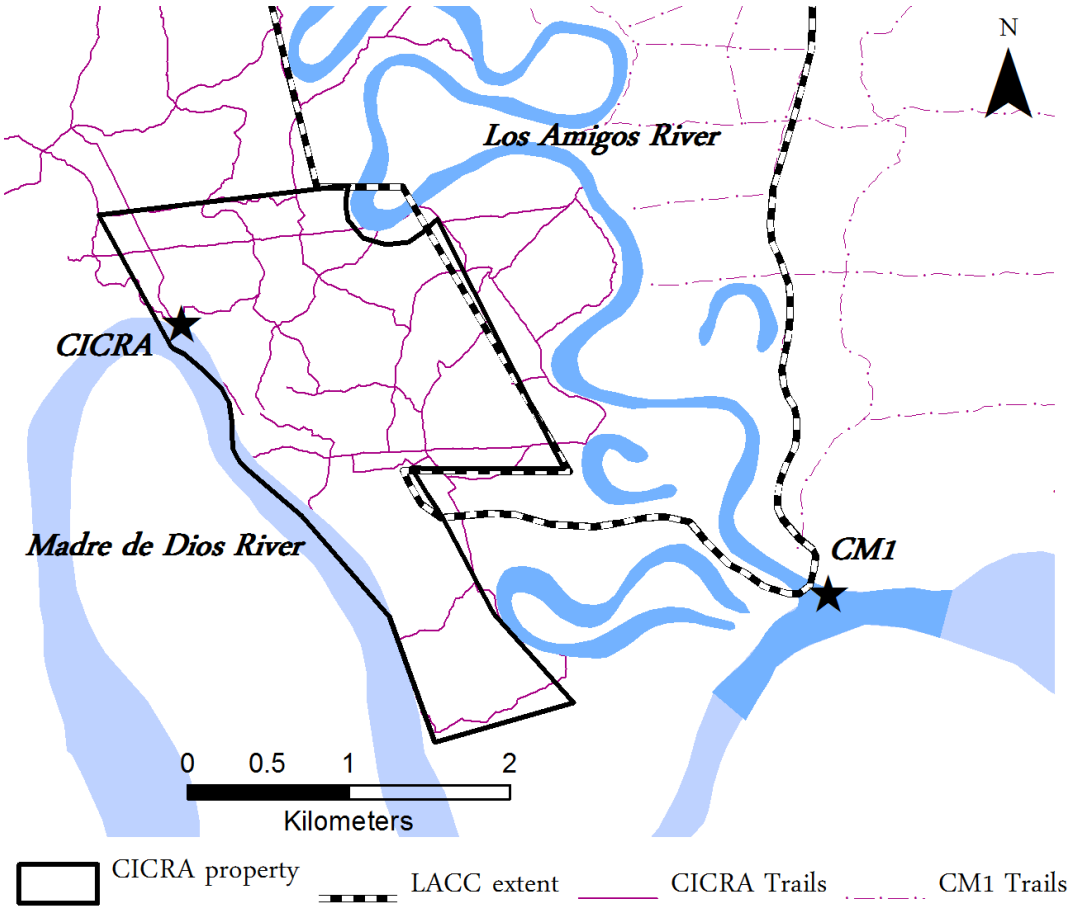


Figure II. 2: A map of the Los Amigos River watershed in southeastern Perú. The map details the Madre de Dios and Los Amigos Rivers, the Los Amigos Conservation Concession (LACC), the trail system at CICRA, the trail system at satellite field station CM1, the CICRA property (outlined in black), and the two field stations (✯). All work for this study was conducted at CICRA alone.

II. 2: Habitat

The forest structure at CICRA is quite varied and can be classified broadly into five major vegetation types: *Woodland forest, bamboo, palm swamp, floodplain, and successional forest*. ***Woodland forest*** includes two types of forest–mature (Fig. II. 3; habitat type A1) and secondary terra firme forest (Fig. II. 3; habitat type A2). The mature forest (similar to that described by Pitman et al. 2001) has a 25-m canopy, with emergent trees up to 35 m tall, and the dominant plant families are Moraceae, Fabaceae, and Cecropiaceae. The secondary woodland terra firme forest is recovering from selective logging, and is 15 to 20 years old. Canopy height is 15 m with 25-m tall emergent trees, and the dominant plant families are Cecropiaceae, Euphorbiaceae, and Melastomataceae (N. Pitman, *pers. comm.*) ***Bamboo*** patches of mostly *Guadua* spp. abound close to the field station, and are also found adjacent to the Los Amigos River (Fig. II. 3; habitat type E) (Olivier 2008).

Permanently flooded ***Palm Swamps*** (Fig. II. 3; habitat types B1, B2) occur west of the airstrip, as well as in the floodplain, with patches of seasonally flooded palm swamp existing throughout the terra firme forest. Mature and disturbed ***Floodplain Forest*** (similar to that described by Gentry & Terborgh 1990) (Fig. II. 3; habitat type A3) have canopies 25 m high with emergent trees up to 35 m tall and are dominated by families Moraceae and Fabaceae (Pitman et al. 2005). Since the field station is located between the Madre de Dios and Los Amigos Rivers, occasional ***Successional Forests*** on the riverbank (Fig. II. 3 habitat type C), largely comprised of Cecropiaceae, are also present.

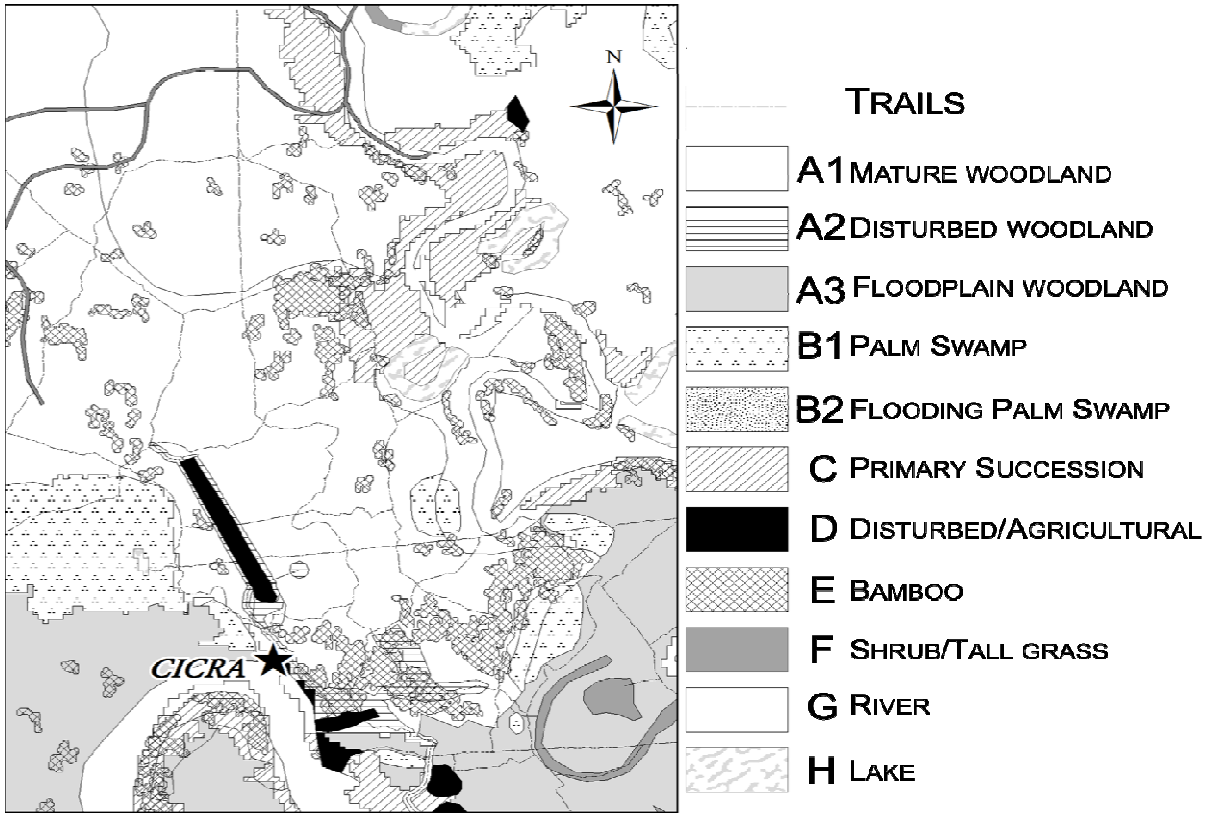


Figure II. 3: Vegetation types at CICRA. **A1** Terrace woodland: mature/old-growth, **A2** Terrace woodland: young/disturbed, **A3** Floodplain woodland, **B1** Palm swamp, **B2** Palm swamp that floods in the dry season, **C** Woodland: primary succession, D Managed/agricultural/disturbed, **E** Bamboo, **F** Shrub/tall grass, **G** River, **H** Lake. Oblong shape in category D in north of CICRA is the airstrip. Map and categories adapted from compilation by Dr. Jonathan Winn (jwinn@durkamwt.co.uk).

II. 3: Climate

Staff members at CICRA have manually collected climate data, including maxima, minima, and rainfall, from November 2000 to the present, on a nearly daily basis (ACA *unpubl. data*). From September 2004 to April 2010, weather data were also collected on an automated weather station (Spectrum Watchdog 700). For consistency, only manually collected temperature and rainfall data are included in the analyses below.

Data from CICRA show two definite seasons during the year – the wet season from October to March, defined as months where average monthly precipitation > 250 mm, and the dry season from April to September, driven by rainfall that is relatively low in the middle of the year (Fig. II. 4). In the wet season, rain occurred from 17 to 25 days per month, and a mean monthly temperature of 24.6°C (*SD* = 0.0) was recorded during this time. During the dry season, mean monthly temperature was 22.8 °C (*SD* = 0.4) and average monthly precipitation was 136 mm (*SD* = 19). When these data are represented as a Walter-Leith climate diagram (1973), where 10°C on the mean monthly temperature scale is set equal to 20 mm of rainfall, mean precipitation remained higher than mean temperature uniformly throughout the year, as expected with tropical rainforest biomes (Fig. II. 4).

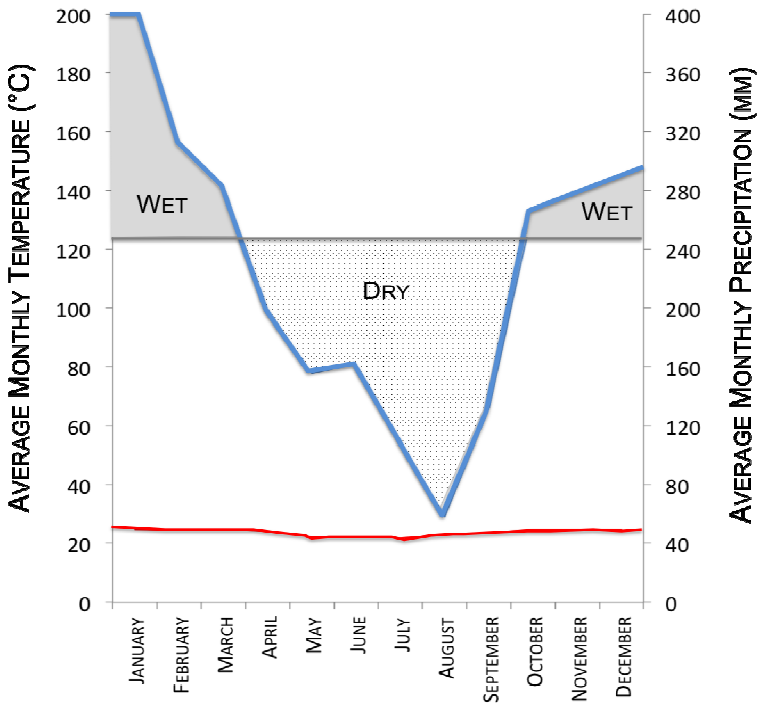


Figure II. 4: Mean monthly precipitation (in blue) and mean monthly temperature (in red) at CICRA. Precipitation remains higher than temperature through the year, as observed in other rainforest systems across the world (Walter 1973). For the purposes of this study, months with an average rainfall > 250 mm (horizontal gray line) are defined as being in the wet season.

Mean daily temperature during 2000-2012 was 23.2 °C (*SD* = 2.6), ranging from 8.5°C to 32.5 °C. Mean monthly temperature was 23.3 °C (*SD* = 1.2), without much variation across the months (range: 21.3 °C to 24.6 °C). Mean total annual rainfall at CICRA was calculated for all years with complete rainfall data available (2001-2003 and 2006-2011). It was observed to be 2584 mm (*SD* = 492), ranging from 1842 mm – 3558 mm. No significant increases or decreases in annual precipitation were detected from 2000 to 2011, for years with available data (Fig. II. 5).

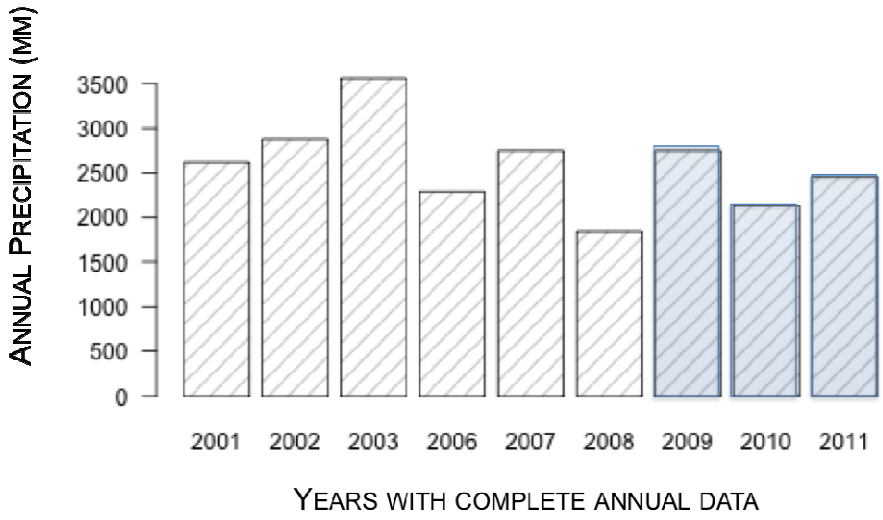


Figure II. 5: The total annual precipitation at CICRA from 2001 to 2011, excluding years with incomplete data (2000, 2004, 2005, 2012). The study duration is highlighted with darker bars, and included 2012.

Weather data collected during the study period itself followed the general trends for this site (compare Figs. II. 4 and II. 6). The driest month in the study period was June 2012 (20 mm of rain), and the wettest month was January of 2010, with *ca*. 491 mm of rain. Precipitation was highest during the months of January and February, for all three years, while mean daily temperature was highest in the months just before this peak precipitation. Further, mean daily temperatures dropped during these wettest months (Fig. II. 6).

II. 3. 1: Friajes

Surges of cold air often occur close to large north-south mountain ranges, such as the Himalayas and the Rocky Mountains (Garreaud 1999). In South America, cold surges called *friajes* (or *friajens* in Brazil), from east of the Andes cordillera, occur reliably throughout the year and are most frequent in the winter months. These sudden temperature drops typically begin when a temporary cold core high-pressure center arrives at the southernmost tip of South America from the Pacific Ocean (Marengo et al. 1997). The cold surge then intensifies as it crosses Argentina, finally arriving at the Madre de Dios region of Perú.

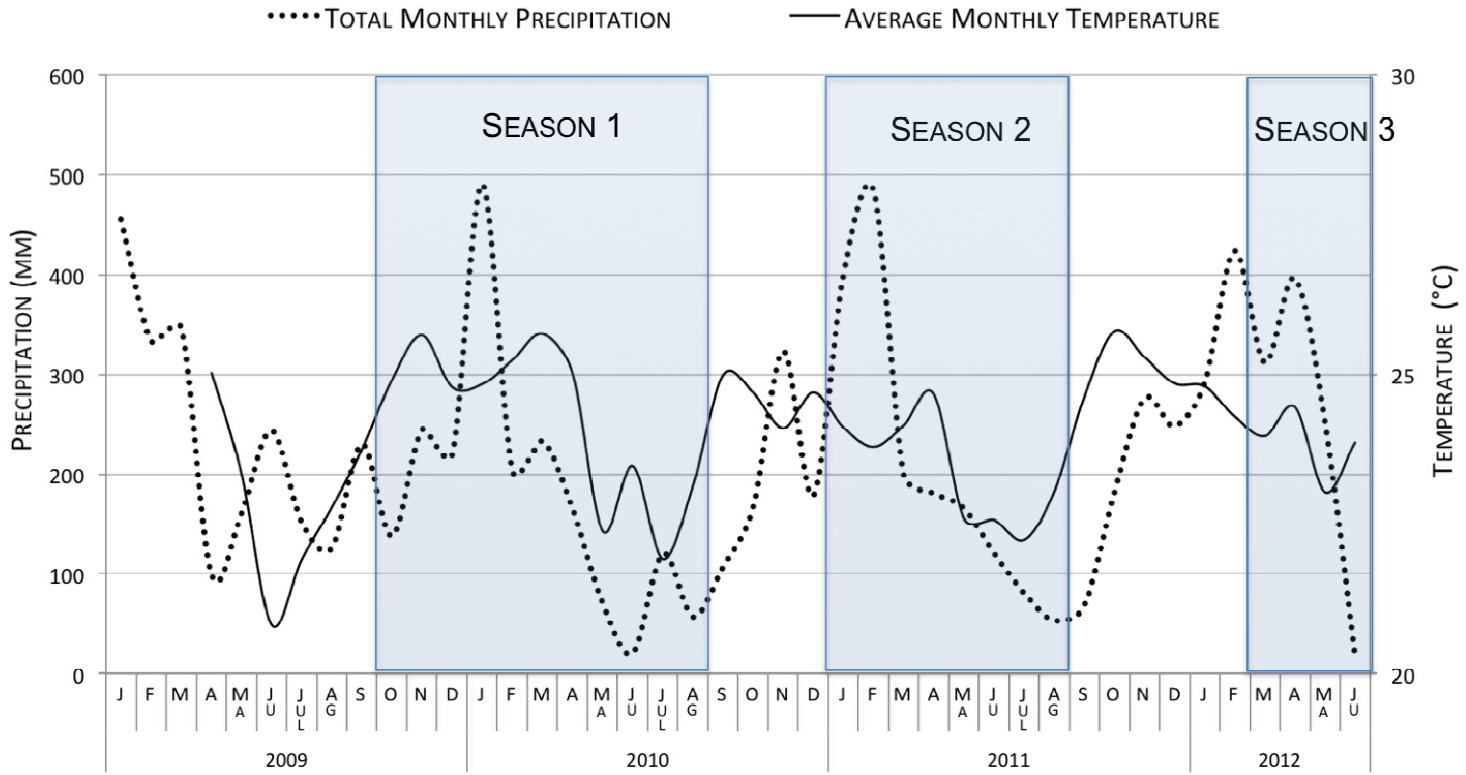


Figure II. 6: Monthly precipitation (mm) (left axis) and average monthly temperature (°C) (right axis) plotted over four years. The study duration is indicated in blue. Monthly precipitation is the sum of rainfall for that month, while average monthly temperature is the mean daily temperature averaged across the days of the month.

Temperatures typically can fall as much as 15°C in 24 h, sometimes remaining low for as long as a week (reviewed in detail by Marengo et al. (1997) and Garreaud (1999)) (M. Watsa, *pers. obs.*). In Brazil, *friajens* have created frosts that impede coffee production and cause considerable economic distress (Marengo et al. 1997). A study of five *friajes* at sites within the same department showed that high-canopy dwelling anurans descended towards the undergrowth to avoid colder temperatures in the canopy (Doan 2004). However, the effects of such events on other wildlife remain largely undocumented.

Pitman, who lived and worked at CICRA for five years, examined *ca.* seven years of daily temperature data available at CICRA and found remarkable stability in the numbers of both types of *friajes* during the winter season, although the lengths of *friajes* varied across the years (2008). I analyzed weather data from this site during the dry season alone (April through September), from 2001 to 2012 (excluding 2005 due to missing data) using criteria developed by Pitman (2008). He defined a *friaje* as two or more days with daily minima ≤ 20°C while a severe *friaje* is two or more days with daily minima ≤ 15°C. Using these definitions, I compared 11 years of available data from this site (2001-2012, excluding 2005) (Table II. 1, Fig. II. 7).

During July of 2010, while this study was being conducted, an unusually cold *friaje* occurred at the study site. Unfortunately, temperature data were not recorded manually at the site during this time. For a period spanning 17 days (16 July – 26 July, 2010, and 30 July – 4 August, 2010) daily minima data were obtained from a weather station located at a satellite field station (CM1) ten minutes downstream from CICRA on the Madre de Dios River (ACA, *unpubl. data*). Data from these sites were considered comparable due to their proximity and the similarity in habitat, forest structure, and data recording methodology.

Table II. 1: Occurrence and attributes of *friajes* at CICRA.

	Year										
	2001	2002	2003	2004	2006	2007	2008	2009	2010	2011	2012
FRIAJES											
Number of *friajes* (2+ days < 20 °C)	10	10	9	4	12	9	9	12	10	12	4
Number of days with minima < 20	50	118	137	135	139	142	147	79	79	68	13
Longest *friaje* (days)	13	70	44	49	24	46	55	21	39	15	6
Average length of *friajes* (days)	45.0	11.8	15.2	33.8	11.6	15.6	16.3	6.6	7.9	5.7	3.3
Lowest minima (°C)	7	14	10	12	11	10	12	9	9	12	16
Months with lowest minima	July	June Aug.	July	June Aug.	July	July	Sep.	July	July	Aug.	May
SEVERE FRIAJES											
Number of severe *friajes* (2+ days <	2	6	5	10	4	9	7	5	3	4	0
Number of days with minima < 15 °C	9	14	27	33	17	35	24	13	16	14	0
Longest severe *friaje* (days)	7	3	9	5	5	6	5	3	8	4	0
Average length of severe *friajes*	4.5	2.3	5.4	3.3	4.3	3.9	3.4	2.6	5.3	3.5	0

Aug. = August; Sep. = September

Daily minima were analyzed from April to September (the dry season) from 2001 to 2010. Data from 2005 are excluded, as they were not recorded for that year. Based on their definitions, severe *friajes* are a subset of *friaje* data.

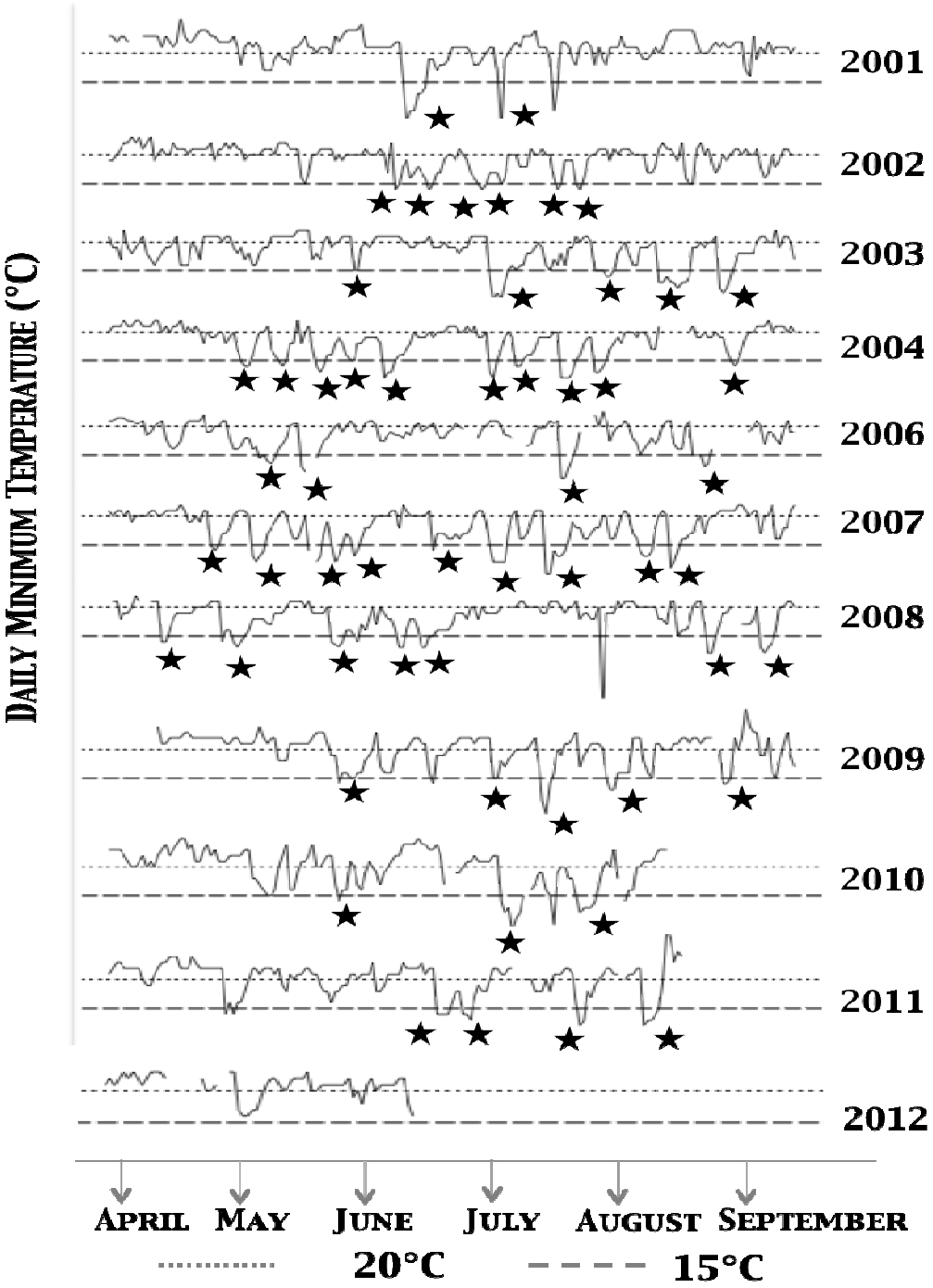


Figure II. 7: Daily minima during the dry season months (April to September) at CICRA per year. Data for 2005 were not recorded. Stars indicate severe *friajes* during this time, defined as two or more days with daily minima ≤15 °C. The dashed lines indicate threshold temperatures of 15 °C and 20 °C (see legend).

Two or more continuous days with daily minima ≤ 20 °C were considered a *friaje*, and when a single day within that range had a temperature > 20 °C, it was considered to be a part of that *friaje*. A break of 2 or more days with temperature > 20 °C was considered a hard break, ending the duration of the first *friaje*. However, for severe *friajes*, a break of 1 or more day with temperature > 15 °C was defined as ending the episode.

At CICRA, the average dry season has a mean of 9.2 ± 2.2 *friajes* and 5.5 ± 2.6 severe *friajes* (Fig. II. 7). The day with the lowest minimum temperature is more likely to fall in July each year, than any other month (Table II. 1). The longest *friaje* spanned 70 days, from May through July, in a single stretch. The coldest severe *friaje* dropped temperatures as low as 7 °C in 2001, but most years, the lowest temperatures achieved range from 9 °C to 12 °C (Table II. 1).

The intensity score of a *friaje* was designed to reflect the effects of both the duration of the *friaje* and the temperature of each day during the *friaje*. The score for each *friaje* was calculated as the sum of the reciprocal daily minima for the duration of the *friaje*, determined by the specifications listed above.

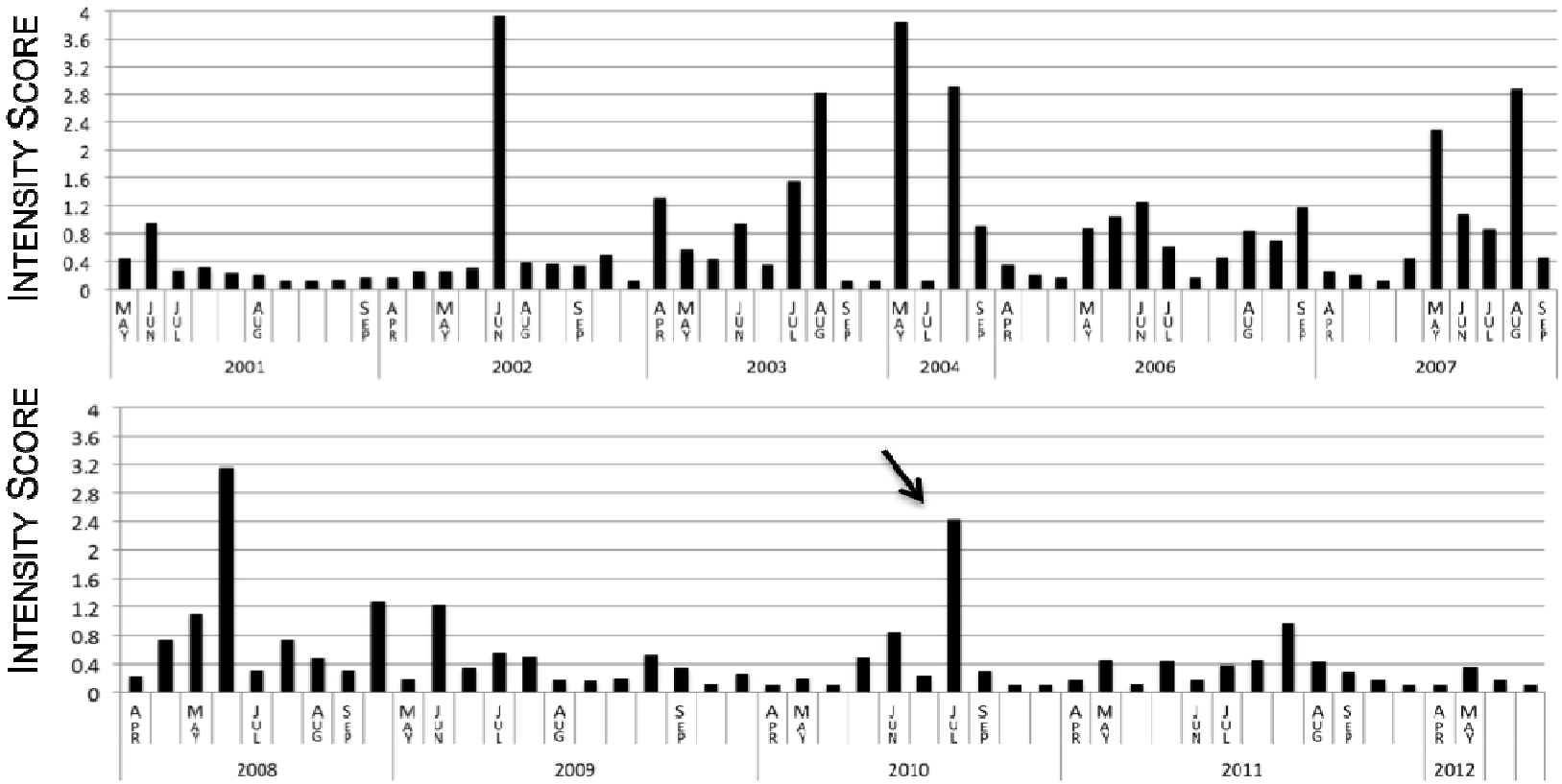


Figure II. 8: Intensity of *friajes* over time (2001- 2012). No daily minima data were recorded for 2005. In general, intensity values increase both when the length of the *friaje* increases and the daily minimum temperature is lower. The arrow indicates the most severe *friaje* observed during this study.

II. 3. 2: Potential Impact on Wildlife

The most intense *friaje* began during the study period for this project in July of 2010, and spanned 39 days, of which 16 had temperatures ≤ 15 °C. No other *friaje* of this magnitude has been observed during the study period, from 2009 to 2012. However, in years preceding this study, not only have there been more such *friajes,* they have also been *friajes* with higher intensities (Fig. II. 8); the effect on wildlife at that time remains unknown. The *friaje* of July 2010 had substantial effects on primates and birds at the site. Several juvenile birds were found dead on the trails, and reports of the death of a juvenile titi monkey (*Callicebus*) were also received from within the LACC (A. Zuñiga, *pers. comm.).* At the study site, one focal group of *Saguinus fuscicollis* vanished immediately after this *friaje* and the breeding female's carcass, with collar intact, was later discovered near the group's most frequented sleeping tree.

There is no question that dangerous weather phenomena such as *friajes* can have life-altering effects on wildlife. It is possible that while *friajes* may create survival bottlenecks in wildlife populations, the animals living here have adapted uniquely to surviving periodic cold temperatures. The focal group of *Saguinus fuscicollis* spent several days within a burrow at the base of a tree, and was never observed to have used this sleep site at any other time, nor did it after the *friaje* had ended. This particular phenomenon has been observed during this study to eliminate a group entirely, which subsequently altered the ranging behavior of groups in the surrounding territories (*cf.* Chapter VII).

II. 4: Primate Community

The primate assemblage at CICRA consists of 11 species in 9 genera, none of which is endemic to Perú (Pacheco et al. 2009) (Table II. 2). Of the five sites that have been surveyed within the Department of Madre de Díos, CICRA has the second highest number of primate species, exceeding counts in the Tambopata-Tavará region, which has flourishing research stations (Table II. 3). Although the IUCN Redlist distribution map for the pygmy marmoset (*Cebuella pygmaea*) includes both CICRA and the LACC, this species is notably absent at CICRA but is present in Manu National Park (la Torre & Rylands 2008). *Lagothrix lagothricha*, the common woolly monkey, which has been seen on the southern bank of the Madre de Dios River (R. Leite Pitman, *pers. comm.*), is also conspicuously absent from CICRA.

II. 4. 1: Study Species

II. 4. 1. 1: *Saguinus fuscicollis weddelli* (Deville, 1849)

Locally abundant, *Saguinus fuscicollis weddelli* has the widest distribution among all subspecies of *S. fuscicollis* and is found in Brazil, Bolivia and Perú (Rylands & Mittermeier 2008). Diagnostic characteristics include distinctive white eyebrows on the forehead, a white muzzle, black forelimbs, torso and tail, rust-red thighs and rump, and a speckled saddle on its middle and lower back (Hershkovitz 1977a) (Fig. II. 9). Infants have white cheek patches and no saddle upon birth but by *ca.* 6 months of age, develop a saddle and fully white muzzle. At this site, this species is commonly found in groups of 3 to 9 individuals in the understory, and from 5 to 15 m high in terra firme, bamboo, and swamp forests (Fig. II. 3 habitats A, B and E). In a unique case, two groups totaling 17 individuals and including 2 sets of twin infants, were found to associate and sleep together for several days during January 2010.

Table II. 2: List of primates observed at the Los Amigos Conservation Concession and CICRA and their conservation status.

Scientific Name	English name	Common Name	CICRA Status [o]	Peruvian Status[a]	IUCN Status	CITES
Family Callitrichidae						
Saguinus fuscicollis weddelli	Saddlback tamarin	Pichico común	C	-	LC[b]	II
Saguinus imperator subgrisiscens	Emperor tamarin	Pichico de bigotes	C	-	LC[c]	II
Callimico goeldii	Goeldi's monkey	Pichico negro	C	NT	VU[d]	I
Cebuella pygmaea	Pygmy marmoset	Leoncillo	E	-	LC[e]	II
Family Atelidae **Subfamily Atelinae**						
Alouatta seniculus	Colombian red howling monkey	Mono coto	C	NT	NT[f]	II
Ateles chamek	Peruvian black spider monkey	Maquisapa	C	VU	EN[g]	II
Lagothrix cana tschudii	Peruvian woolly monkey	Mono chorro	E	VU	EN[h]	II
Subfamily Pitheciinae						
Aotus nigriceps	Peruvian night monkey	Musmuqui	C	-	LC[i]	II
Callicebus brunneus	Brown titi monkey	Tocón	C	-	LC[j]	II
Pithecia irrorata irrorata	Grey's bald-faced saki	Huapo	C	-	LC[k]	II
Family Cebidae						
Cebus albifrons cuscinus	Shock-headed capuchin	Machín blanco	C	-	NT[l]	II
Cebus macrocephalus	Large-headed capuchin	Machín negro	C	-	LC[m]	II
Saimiri boliviensis boliviensis	Bolivian squirrel monkey	Fraile, Huasa	C	-	LC[n]	II

Species confirmed through direct observations are indicated as “C”, and those expected but not seen are “E”. The International Union for the Conservation of Nature (IUCN) Status: LC = Least Concern, VU = Vulnerable, NT = Near Threatened, EN = Endangered. The Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) specifies the following: Appendix I: species threatened with extinction; Appendix II: species not necessarily threatened, but in which trade must be controlled to avoid utilization incompatible with survival; and Appendix III: species that are protected in at least one country, which has requested assistance from CITES Parties in controlling trade in that species. References: [a] INRENA (2004), [b] Rylands and Mittermeier (2008), [c] Rylands and Mittermeier (2012), [d] Cornejo (2008), [e] de la Torre and Rylands (2008), [f] Boubli et al. (2008a), [g] Wallace et al. (2008b), [h] Boubli et al. (2008b), [I] Cornejo and Palacios (2008), [j] Veiga et al. (2008), [k] Marsh and Veiga (2012), [l] de la Torre et al. (2008), [m] Rylands et al. (2008), [n] Wallace et al. (2008a), [o] Pitman (2008).

Table II. 3: Comparative listing of primate species in and around the Los Amigos Conservation Concession and CICRA.

Species	CICRA	Tambopata-Tavará	Explorer's Inn	Cuzco Amazónico	Cocha Cashu /Pakitza	Balta
Source		1	1	2	2,3,4,5,6	2
Family Callitrichidae						
Saguinus fuscicollis	X	X	X	X	X	
Saguinus imperator	X				X	X
Callimico goeldii	X				X	
Cebuella pygmaea					X	
Family Atelidae						
Subfamily Atelinae						
Alouatta sara/seniculus	X	X	X	X	X	X
Ateles chamek	X	X			X	X
Lagothrix cana tschudii		X		X	X	X
Subfamily Pitheciinae						
Aotus nigriceps	X	X	X	X	X	X
Callicebus brunneus	X	X	X		X	X
Pithecia irrorata	X				X	X
Family Cebidae						
Cebus albifrons cuscinus	X	X	X	X	X	X
Cebus apella/ macrocephalus	X	X	X	X	X	X
Saimiri boliviensis boliviensis	X	X	X	X	X	X
Number of species	11	9	7	7	14	10
Kilometres from CICRA*	---	83	92	112.5	162	298

* Pitman (2008), 1: Foster et al. (1994), 2: Voss and Emmons (1996), 3: Janson and Emmons (1990), 4: Solari et al. (2006), 5: Terborgh (1983), 6: Terborgh et al. (1985).

Figure II. 9: *Saguinus fuscicollis weddelli* and *Saguinus imperator subgriscicens* at CICRA, displaying their distinctive appearance of heightened morphological homogeneity.

Births in *S. fuscicollis* typically occur from September to January at this site, and twinning is apparent although not all infants survive the rainy season. Dispersal of individuals was observed primarily in June and July. Groups of *Saguinus fuscicollis* are observed traveling and associating with *S. imperator*, *Callicebus brunneus*, and *Callimico goeldii,* and rarely, *Saimiri boliviensis*.

Other studies within Perú utilizing line transect survey methods have estimated population densities for this species ranging from 2.4 – 56.8 individuals per km^2, with a mean of 16.5 ± 3.4 individuals per km^2 (Table II. 4). Given a surveyed area of 500 ha or 5 km^2, I used actual counts of groups in the area and calculated a population density of 18.5 individuals per km^2 and a group density of 2 groups per km^2. Population density at this site was comparable to those reported elsewhere, and much higher than densities at neighboring areas such as Cocha Cashu and EcoAmazonía Lodge (10.8 individuals per km^2), and the Tambopata Research Center (6.9 individuals per km^2) (Table II. 4).

Table II. 4: List of population densities of *Saguinus fuscicollis* recorded at neighboring sites in Perú.

Site Name	***Saguinus fuscicollis***	Reference
Panguana	2.4	Freese et al. (1982)
Upper Nanay	4.8	Freese et al. (1982)
Sachavacayoc	5.6	Kirkby et al. (2000)
Tambopata Research Center	6.9	Kirkby et al. (2000)
Explorer's Inn	7.4	Kirkby et al. (2000)
Orosa	9.0	Freese et al. (1982)
Río Itaya	10.5	Aquino et al. (2007; 2009)
Cocha Cashu	10.8	Freese et al. (1982)
EcoAmazonoia Lodge	10.8	Kirkby et al. (2000)
von Humboldt	13.8	Freese et al. (1982)
Samiria	15.0	Freese et al. (1982)
Cuzco Amazónico Pueblo	15.2	Kirkby et al. (2000)
CICRA	***18.5***	***This study***
Tahuayo-Blanco	21.7	Puertas et al. (1996)
Camp Callicebus	22.8	Freese et al. (1982)
Itaya	29.4	Freese et al. (1982)
Yavarí-Mirí	37.8	Puertas et al. (1996)
San Miguel *	56.8	Aquino and Calle (2003)

* It is possible that the calculation of density at San Miguel is faulty

II. 4. 1. 2: *Saguinus imperator subgrisescens* (Lönnberg, 1940)

The emperor tamarin (*Saguinus imperator*) has two major subspecies, *S. imperator imperator,* which is primarily found in Brazil (although it extends into Perú along the River Acre), and *S. imperator subgrisescens,* more commonly found across Perú (Rylands & Mittermeier 2012). Diagnostic characteristics of adults of this species include a white elongated mustache, black mask across eyes, grey trunk and shoulders and outer limbs, and rusty orange underside and tail (Hershkovitz 1979) (Fig. II. 9). *Saguinus imperator subgriscecens* is most easily distinguished from *S. i. imperator* by the lack of black chin patch.

The subspecies at CICRA, *S. i. subgriscecens*, can be found in groups of 2 to 7 individuals in the understory and from 10 to 20 m high in the canopy of terra firme and bamboo forests (Fig. II. 3, habitats A, B and E). An early study of 7 groups of this species at CICRA revealed that group sizes average around 5 adults, typically including only a single adult female per group, although a population density estimate was not provided (Aragón 2007). Primarily twin infants were born in October through February. Dispersal of individuals was observed between May and August (Aragón 2007).

I found a group density of 1.5 groups per km^2 and a population density of 7.5 individuals per km^2 at this site. Other estimates of population density per km^2 within the country for this less-known species include 5.4 individuals (Freese et al. 1982). At CICRA they were observed to travel and associate with *S. fuscicollis*, *Callicebus brunneus*, and *Callimico goeldii*.

II. 4. 2: Other Primate Species

II. 4. 2. 1: *Callimico goeldii* (Thomas, 1904)

Callimico goeldii or Goeldi's monkey has been observed in Perú, Brazil and Bolivia, with over 75% of its range lying within Perú (Cornejo 2008). Its generally cryptic and elusive nature can greatly reduce its detectability using standard line transect methodology sites (Watsa et al. 2012). Although very little is known about its genetic population structure, a recent study on

captive populations suggests the possibility of the existence of more than one subspecies (Vàsàrhelyi 2002). Diagnostic features include an all-black pelage, a bobbed mane with a pompadour on the top of the head, and pigmented facial skin (Hershkovitz 1979).

At CICRA, *Callimico goeldii* has been observed on only 17 occasions in the duration of this study, in association with *Saguinus fuscicollis* and *S. imperator* in all instances save one. Watsa *et al.* (2012) estimate a maximum of two groups of three *Callimico goeldii*, including an adult pair and a single juvenile, although it can only be certain that one such group exists due to the low frequency of sightings. Whether these animals are resident at CICRA or range more broadly is unknown. This leaves their population density at best at *ca.* 0.4 groups per $km^{2,}$ which is one-fifteenth to one-thirtieth of the density of *Saguinus fuscicollis* within the same region, and is consistent with findings at sites in Bolivia (reviewed in Rehg 2007). Life history data of these animals at this site is currently unavailable due to their low densities.

II. 4. 2. 2: *Alouatta seniculus* (Linnaeus, 1766)

Alouatta seniculus, or the Colombian red howler, is described by the IUCN as extending as far south in Perú as the Inuya River (Boubli et al. 2008a); however, it is definitely found further south at Manu National Park and CICRA within the Department of Madre de Dios (Terborgh et al. 1985). This species of howler monkey, rarely seen or heard at CICRA, appears to be recovering from hunting pressures on it in the early 1980s, with more frequent sightings each year. *Alouatta seniculus*, with their brick-red pelage, have been observed in groups of two or more individuals, >20 m high in terra firme and floodplain forests (Fig. II. 3, Habitats A and E), and at least one group is relatively habituated to human presence at this site. Groups may through fairly large ranges since their distinctive vocalizations at dawn are only audible for a few days at a time at the field station, despite their great vocal transmission range.

II. 4. 2. 3: *Ateles chamek* (Humboldt, 1812)

Ateles chamek, or the Perúvian black spider monkey is found in southern Perú, as well as Brazil and Bolivia (Wallace et al. 2008b). Distinctive characteristics include a black body with black face except for pale pink circumocular rings, and a pink nose and maxilla (Kellogg 1944). *Ateles chamek* at CICRA have been seen in groups of up to 9 individuals, in the highest levels of the canopy of terra firme and floodplain forests (Fig. II. 3 Habitats A, B), although lone male spider monkeys have been observed as well. On one occasion a single female spider monkey was observed traveling and foraging with a group of *Cebus macrocephalus* and *Samiri boliviensis* for > 1 h. Spider monkeys at CICRA are as rarely seen as howler monkeys, although sightings have increased over the last few years. As with *Alouatta seniculus*, this may be a consequence of hunting pressures of the past now lifting.

II. 4. 2. 4: *Aotus nigriceps* Dollman, 1909

Aotus nigriceps is fairly common throughout the Amazon, and is found in south and central Perú (Cornejo & Palacios 2008). Distinctive characteristics include a grey dorsal pelage, orange ventral pelage extending to the throat, and white tufts above the eyes separated by a black widow's peak (Groves 2001). This species is fairly common at this site, and was observed active at night and during the day. Groups of up to 4 individuals have been observed roaming >15 m in terra firme forests (Fig. II. 3, Habitats A1 and A2), and several group sleeping sites were identified at 10 to 15 m high in thick bramble. Infants were observed in January, in the middle of the wet season.

II. 4. 2. 5: *Callicebus brunneus* (Wagner, 1842)

The current taxonomic status of the species at this site is under some debate since the release of a taxonomic review of the titi monkeys by van Roosmalen et al. (2002). The discovery of *Callicebus aurepalatti* in western Bolivia has led some to speculate that its range may extend to the LACC, and further work on identifying them is underway (Vermeer 2009; Wallace et al. 2006). However, the species at this site is generally thought to be *Callicebus brunneus*, which is

part of the *moloch* species group. This species is found in Brazil, Bolivia and a small section of southeastern Perú (Veiga et al. 2008). Distinctive characteristics include dark brown fluffy pelage, black faces and orange eyes, with long straight brown tails tipped in white, with a fair amount of variation in tail pelage at CICRA (Groves 2001). Information on *C. brunneus* at this site comes from a study on the pair bond between males and females (Nole Bazán 2008) and another on parasite prevalence in this species (Lawrence 2007). Groups are found in terra firme forests, both disturbed and primary, as well as in bamboo (Fig. II. 3 Habitats A, C, D and E) and consist of a single adult male and female and usually two offspring, although lone individuals are also observed on occasion. Lawrence (2007) estimated average home range size is 2.5 ± 0.5 ha, and within the study site of 0.41 km^2 or 41 ha, population density was an estimated 41 to 51 individuals per km^2. Further, births were found to occur seasonally from August to September (Lawrence 2007).

II. 4. 2. 6: *Pithecia irrorata irrorata* Gray, 1842

Pithecus irrorata irrorata is wide-ranging, present in Brazil, Bolivia and southeastern Perú (Marsh & Veiga 2012). Distinctive features of this primate at CICRA include a very thick, mottled, grey and black pelage, black faces and feet, and long bushy tails. Two major studies of this species have been undertaken at this site (Adams 2009; Palminteri & Peres 2012). *Pithecia i. irrorata* is found in woodland terra firme forests and palm swamps (Fig. II. 3, Habitats A1, 2 and B) in groups of 4 to 6 individuals, usually with a single adult pair and dependent offspring, although one group included two adult females (Adams 2009). During this study, we observed this species in groups of 1-6 individuals. It is important to note that the Tambopata-Candamo Reserve is lacking any *Pithecia* sp. (Voss & Emmons 1996), while Manu National Park has *P. monachus*, a different species from that observed at CICRA (Solari et al. 2006; Terborgh et al. 1985).

II. 4. 2. 7: *Cebus albifrons cuscinus* Thomas, 1901

Cebus albifrons cuscinus is found in Perú, as well as Bolivi, Brazil (Acre and Amazonas), and Ecuador (la Torre et al. 2008). Diagnostic characteristics include pale brown torso, crown dark brown or black, contrasting with body, with long fur in comparison with *Cebus macrocephalus* (Groves 2001). At CICRA it has been seen in terra firme forest as well as bordering palm swamps or aguajales (Fig. II. 3, Habitats A1 and B). It was observed rarely, but always in groups of 10 or more individuals between 20-30 m high in the canopy. In comparison with the other species of capuchin at this site, *Cebus macrocephalus*, it is less common and rarely seen in association with *Saimiri* sp. As yet, data on ecology and reproduction are lacking for this species at this site.

II. 4. 2. 8: *Cebus macrocephalus* Spix, 1823

Cebus macrocephalus, recognized as *Cebus apella macrocephalus* in other taxonomies (Groves 2001), is observed in the Peruvian Amazon, north of the Madre de Dios River (Rylands et al. 2008). Diagnostic characteristics include a dark brown body with dark dorsal stripe, and a black tuft of hair above the forehead (Groves 2001). It is the most commonly seen medium-sized primate at CICRA, found anywhere from 10 to 30 m high in the canopy of terra firme and floodplain forests (Fig. II. 3, Habitats A, B and E). Infants were first observed in December at the beginning of the wet season. At this site, *Cebus macrocephalus* is usually found in groups of >25 individuals traveling together with *Saimiri boliviensis*, which together may include over 80 adult individuals, and at least two such groups have been identified at CICRA.

II. 4. 2. 9: *Saimiri boliviensis boliviensis* (I. Geoffroy & de Blainville, 1834)

Saimiri boliviensis boliviensis is present in Bolivia, Brazil (Acre and Amazonas) and southeastern Perú (Wallace et al. 2008a). Distinctive characteristics include orange-beige dorsal pelage, with white fur ventrally, white ears, white rings around black eyes, and a black snout and head with a clear widow's peak in black on the forehead. It is most commonly found in groups of more than 70 adult monkeys, usually traveling and foraging with *C. macrocephalus*

in terra firme and floodplain forests (Fig. II. 3, Habitats A, B and E) (63% of sightings in Season 1 were with *Cebus*). One count in January 2013 included 151 adults and infants roaming with 10 *Cebus macrocephalus*. This species is occasionally observed roaming in smaller groups (3 to 5 individuals) without *Cebus* and on one occasion, four individuals were seen traveling with three *S. f. weddelli* for over 50 minutes in swamp forest. Infants were observed throughout the year.

II. 5: The Mammal Community

The mammal community at CICRA has not been comprehensively described to date, but shares some similarities with that of neighboring Manu National Park (Terborgh et al. 1985). The LACC has a large and varied population of mammalian wildlife (Table II. 5). The IUCN has not evaluated most of the *ca*. 4330 species of plant and wildlife in the Los Amigos Conservation Concession (Pitman 2008), including at least 26 vulnerable or endangered species (Table II. 5).

Table II. 5: A preliminary list of globally threatened of near threatened species in the Los Amigos Conservation Concession, updated based on the IUCN Red List of 2012 modified from Pitman (2008).

Common Name	Scientific Name	Global Conservation Status
PLANTS		
Brazil Nut	*Bertholletia excelsa*	Vulnerable
--	*Caryocar amygdaliforme*	Endangered
Tropical Cedar	*Cedrela fissilis*	Endangered
Red Cedar	*Cedrela odorata*	Vulnerable
Fine-leaf Wadara	*Couratari guianensis*	Vulnerable
Bigleaf Mahogany	*Swietenia macrophylla*	Vulnerable
REPTILES		
South American Tortoise	*Geochelone denticulate**	Vulnerable
Yellow-spotted River Turtle	*Podocnemis unifilis*	Vulnerable
BIRDS		
Black-and-white Tanager	*Conotrhaupis speculigera**	Near Threatened
Rufous-fronted Antthrush	*Formicarius rufifrons*	Near Threatened
Elusive Antpitta	*Grallaria eludens*	Near Threatened
Harpy Eagle	*Harpia harpyja*	Near Threatened
Crested Eagle	*Morphnus guianensis*	Near Threatened
Amazonian Parrotlet	*Nannopsittaca dachilleae*	Near Threatened
Orinoco Goose	*Neochen jubata*	Near Threatened
Blue-Headed Macaw	*Propyrrhura (Ara) couloni*	Vulnerable
Peruvian Recruvebill	*Simoxenops ucayalae*	Near Threatened
MAMMALS		
Goeldi's Marmoset	*Callimico goeldii*	Vulnerable
Shock-headed Capuchin	*Cebus albifrons capuscinus*	Near Threatened
Pacarana	*Dinomys branickii*	Vulnerable
Giant Anteater	*Myrmecophaga tridactyla*	Vulnerable
Jaguar	*Panthera onca*	Near Threatened
Giant Armadillo	*Priodontes maximus*	Vulnerable
Giant Brazilian Otter	*Pteronura brasiliensis*	Endangered
Bush Dog	*Speothos venaticus*	Near Threatened
Lowland Tapir	*Tapirus terrestris*	Vulnerable

An asterisk (*) indicates unchanged statuses from the original document of 2008.

II. 6: Project Timeline and Participants

This project was conducted over three field seasons: Season 1 – November 2009 to August 2010, Season 2 – January to August 2011, and Season 3 – March to August 2012. In all seasons, the research team included a field guide, a local veterinarian, and myself, although the full team was not all present at all times. Through an organization named PrimatesPeru, created for this project to provide fundraising and volunteer support, volunteer participants were recruited to act as field assistants. They included 8 volunteers in Season 1, 9 volunteers in Season 2 and 6 in Season 3. All seasons were conducted in conjunction with G. Erkenswick, a biologist affiliated with the University of Missouri in Saint Louis, and in 2011 and 2012, Dr. Jennifer Rehg of Southern Illinois University- Edwardsville also collaborated on this work. Further details on the project team can be found at www.primatesperu.org.

II. 7: A History of Threats to the Region

CICRA is located just a short distance from the confluence of the Madre de Dios and Los Amigos Rivers (Fig. II. 1). A compendium of historical literature of the Los Amigos area by Pitman (2008), indicates that an indigenous population referred to as the *Mashcos* lived near the mouth of the Los Amigos River. After several clashes between rubber tappers and this population, they dispersed to an as yet unknown area leaving behind a farm plot of 7 hectares of fruit trees and crops occupied from 1974 to 1981. The family that worked this land sold it to a mining company, which used the station as a base for exploration of the area until 1999. Although as many as 120 men lived at CICRA until 1985, only a handful of people occupied the camp from after that point. The property was finally purchased in 2000 by the Associación para la Conservación de la Cuenca Amzónica (ACCA), which runs the field station today.

Due to its complex history of occupation by miners, the actual impact of their stay on the wildlife and ecology of the area is hard to measure. During its earlier existence, workers hunted and fished in the area, consuming deer, peccaries, tapirs, agoutis, monkeys, and large birds

(Pitman 2008), and it is fortunate that for most of the 1990s the camp remained nonfunctional, and so hunting declined. Estimates of logging impacts on the LACC during the early years of ACCA's ownership indicate approximately 1 tree felled per 100 ha, typically either Brazil nut (*Bertholletia excelsa*) or cedar (*Cedrelinga cateniformis*), so the same may be assumed for CICRA itself.

This measure, even when doubled, remains < 15% of the natural background rates of large tree mortality in tropical forests (assumed to be 2%) (Pitman 2008). A report by ACCA to the National Park Service (then INRENA, now MINAG) contained estimates of 12,884 kg of bushmeat being harvested in the Los Amigos watershed from 2001 to 2002 (ACCA 2002; Schulte-Herbrüggen & Rossiter 2003). The actual field station and the ~500 ha around it (the focus of this study) were not affected by hunting during this time. However, an estimated 206 *Ateles belzebuth* and 107 *Alouatta seniculus* were extracted from the Conservation Concession during the early years of ACCA's management of the site (ACCA 2002). By 2004, with the institution of a ranger station at the mouth of the river that blocked access to the entire Conservation Concession to those without permission, hunting outtake was brought down to zero (Pitman 2008).

In November of 2009, at the start of this study, the Peruvian government declared a mining embargo in the department of Madre de Dios, resulting in the threat of a strike by gold miners; subsequently, our research team evacuated to Puerto Maldonado for ten days. In 2009, travelers up the Madre de Dios River on their way to CICRA were always within sight of at least one mining operation along the riverbank. A second strike in March 2010, caused the evacuation of all but two team members. Although no attempt was made by miners to approach the station, the situation remained in a tense standoff. At the beginning of Field Season 2, in January of 2011, the Peruvian government actually detonated bombs within three large, illegal mining operations along the Madre de Dios River. Subsequently, very few miners were observed

on the river and a second strike followed in February, causing yet another evacuation. The most violent mining strike we have observed thus far occurred in February 2012, but although the situation was volatile, it was restricted entirely to protests in the town of Puerto Maldonado. Gold mining continues to be a threat to the surrounding area, due to high levels of mercury used to collect gold particles from the silt. The mercury is then burnt off, only to deposit in particles within a 10-m radius, proving a long-term health hazard to the miners and the wildlife in the area (Gutleb et al. 1993).

II. 7: Conservation Impact

Previous hunting pressures at this site are almost certainly responsible for the low densities of *Alouatta* and *Ateles* spp., as these populations are purportedly flourishing further up the Los Amigos River within the LACC (A. Zuñiga, *pers. comm.*); however, they appear to be slowly recovering in the CICRA area. Situated between Manú and Alto Purús Reserves in the west, and the Tambopata-Candamo and Bahuaja-Sonene Reserves in the east, the LACC provides a crucial corridor linking these nationally protected areas. Although located in the buffer zone of Manú National Park, gold mining and logging ventures increasingly deplete the surrounding areas of wildlife, obstructing the best efforts of organizations like the Amazon Conservation Association to keep this corridor intact. Little research involving long-term studies of primates has taken place at the LACC (Adams 2009; Aragón 2007; Lawrence 2007; Nole Bazán 2008; Palminteri & Peres 2012), and more information on this diverse population can strengthen the argument for protecting the corridor. In particular, research is sorely needed on little known *Callimico goeldii* and *Pithecia irrorata*, and evaluations of populations of *Ateles* and *Alouatta* spp. as they respond to relaxed hunting pressures. Each year the ACCA requires upwards of $250,000 to keep the station running and the park rangers paid, and PrimatesPeru has contributed nearly $65,000 towards that goal through site fees during the course of this study (2009-2012).

II. 8: Significance of CICRA

CICRA has several unusual features that make it an ideal site for the study of callitrichid biology and ecology. It is located within the buffer zone of Manu National Park, and is adjacent to the Los Amigos Conservation Concession, both receiving protection from either the Peruvian government or the Amazon Conservation Concession. This sustained protection permits a capture and release program that uses trapping methodology, which in less protected areas could be appropriated for the hunting of primates habituated to traps. Its population of primates, although previously hunted in the 1990s, is remarkably habituated to observers despite only a handful of previous studies at this site. In fact, this hunting pressure in the past has resulted in skewed population density that favors the smaller primates, which are less likely to be hunted, over larger, more commonly consumed animals. CICRA's population of *Ateles* and *Alouatta* are still recovering from these pressures and are present in only low densities within the property. On the other hand, CICRA boasts a density of *Saguinus* spp. far greater than the surrounding areas, including Manu National Park. It is possible that the removal of these large-bodied primates has allowed for a much higher density of callitrichids at this site.

Situated as it is, between the Manu National Park and the Tambopata and Buahaja-Sonene protected areas, CICRA and the adjacent LACC form a crucial corridor connecting two otherwise isolated rainforest populations. Not only does this affect wildlife biodiversity and density, but the uncontacted human tribes known to exist northwest of the field station, within the LACC, are also buffered from human exploitation from this protection of the land. The incredible naiveté of the tamarin population, along with their high densities in the area, provide a unique opportunity to examine callitrichid biology through a capture and release program.

Chapter III: Modifications of a Field Protocol for the Capture and Release of Callitrichids

III. 1: Introduction

Captive studies of nonhuman primates have the advantage of revealing details of physiology and morphology that are impossible to discern through direct observation in the wild. Furthermore, they allow for the study of known individuals, which is a simple benefit, yet with profound implications. Working with identifiable primates allows for an investigation to be conducted at the level of the individual and not the group, producing data on factors such as group membership and the fates of dispersing individuals. In the case of some primate genera, such as the large-bodied, visually distinct *Brachyteles* (Strier et al. 2006), observers can become proficient in instantaneously identifying habituated individuals. Many arboreal primates, however, given the decreased visibility under the rainforest canopy, are challenging to locate and identify (Glander et al. 1991). Even with animals that frequent lower forest strata, morphological homogeneity renders individuals of some species virtually indistinguishable from each other (Fernandez-Duque 2003). Some species of primates also do not possess obvious indicators of reproductive state or sexual maturity, preventing consistent identification of individuals by their reproductive status.

Despite the advantages of observing animals at close-quarters and in controlled environments, captive studies, which can establish fundamental characteristics of a species, are limited by small sample sizes and often cannot describe the range of variation of a species' traits. These studies cannot replicate conditions in the wild to their full extent, as their results are affected by captivity itself, and consequently their outcomes cannot always be readily applied to wild populations. Furthermore, only a fraction of the biodiversity of the primate order is represented in captivity, thus limiting the scope of our knowledge to those species that, either as a consequence of history or their specific mating conditions, are successfully bred in captivity. One solution to this problem is the use of mark/recapture or capture-and-release programs on

free-ranging populations of primates that allow for the placement of identification tags on individuals.

The implementation of a capture-and-release program brings with it a veritable wealth of information on free-ranging primates (Jolly et al. 2011; Sapolsky & Share 1998). Such programs provide opportunities for the collection of health data that normally remain unknown for wild primates. Physical examinations can yield information on dental condition and wear, reproductive state, and physical wellbeing, while samples for genetic and parasite analyses can also be recovered. The placement of radio-collars on even a single individual in a group can provide great insight into the use of space by free-ranging primates (Campbell & Sussman 1994). The implementation of these programs, however, is not without its complications (Sapolsky & Share 1998).

III. 1. 1: Risks

There are some concerns that arise when first attempting to capture a previously untouched population of primates. First, there is immense variation between primate species in habitat, body mass, social organization and feeding ecology, making a protocol used for one species entirely unsuitable for another. Therefore, protocols must be species-specific to be successful. Second, comprehensive records of endorsed or accepted trapping protocols are not commonly available or published in the literature, resulting in the often unsuccessful testing of methodologies that can, in retrospect, appear ill-advised and subject to much criticism. It is also quite possible that animals undergoing capture, which does cause elevated stress hormones (e.g. Rodas-Martínez et al. 2012), would retain a memory of the event and subsequently avoid contact with observers, effectively disrupting habituation.

Depending on whether individuals or groups are captured, the separation of individuals from their groups for sample collection, or processing, could unsettle social standings and hierarchies, potentially altering social organization while specific members are being processed

(Brett et al. 1982; Sapolsky & Share 1998). Most importantly, the increased proximity between humans and animals during processing could pose a real danger to the health of a wild primate due to increased disease risks (Fedigan 2010). Capture-and-release programs that utilize darting methodologies can sustain risk to animals either from darts that miss the targeted body area or, in the case of arboreal primates, injuries sustained as the animals descend from the trees to the ground (Cunningham & Setchell 2012). Special care must be taken to avoid these problems, making darting of primates safer and less complicated for terrestrial rather than arboreal primates (Fernandez-Duque 2003; Sapolsky & Share 1998).

Certainly, these are major concerns to be considered during the design of a trapping protocol, but there are prescribed ways to mitigate many of these risks. The United States Department of Agriculture specifies categories of reporting handling of animals in the wild, and the capture of animals in live traps with no more invasive methodology than a peripheral blood draw is supported by care guidelines specified by the American Society of Mammalogists (Category C Sikes & Gannon 2011). These guidelines specify common reasons for the capture of wild animals, including "livetrapping to tag (with radiotransmitters, necklaces, ear tags, or passive integrated transponder tags), mark (number, band, hair color, freeze brand, ear tag, or toe clip), or collect tissue" (Sikes & Gannon 2011). They advocate that live trapping protocols provide adequate protection for the animals from temperature extremes and predation. Traps should be designed to avoid capturing nontarget animals. The number of traps set at any time should not be higher than the ability of the field team to monitor them regularly, and small mammal traps should be checked every 1.5 hours to avoid injuries or mortalities. Trained individuals should conduct necessary chemical immobilization, with experience in the administration of anesthetics, tranquilizers, sedatives, and antidotes in the appropriate doses (Fowler 2008; Kreeger 2007; West et al. 2007). Finally, sedated animals should be monitored closely and released only when they have regained full consciousness and locomotion (Sikes & Gannon 2011).

Primate studies indicate that the safe use of an anesthetic can blur the memory of an event (see Sapolsky & Share 1998), and accompanied by the careful reunion of individuals to their group and the incorporation of safety precautions to prevent disease transmission, alleviate the overall risk to the animal. Studies involving recaptures advance that a verified protocol provides minimal negative impacts of capture-and-release in the long-term (see Jolly et al. 2011).

III. 1. 2: A History of Capturing Primates in Perú

Primates have been captured for centuries for viewing in zoos, museum specimens, pets, or more recently, as laboratory research animals. When certain species were discovered to be ideal laboratory subjects for significant research into disease, such as the owl monkeys (*Aotus spp.*) for malaria (Diaz et al. 2000), large-scale capture programs ensued to obtain sufficient numbers of animals for research laboratories the world over (Nijman et al. 2011). No single country exported more primates than India, with *ca.* 50,000 primates leaving per annum through the 1960s (Southwick & Siddiqui 2001). Today, China is the largest exporter of primates, given India's relatively new ban on all exportation of Rhesus macaques from the country (Nijman et al. 2011). However, Peru came in a close second, exporting *ca.* 30,000 primates per annum in the sixties (Smith 1978).

Between 1961 and 1971, *ca.* 300, 000 live primates were exported from Peru until exports were banned in 1973 (Smith 1978). Since up to 4 animals died for every one that survived exportation (Grimwood 1968), the true extent of the capture program is staggering. Due to the involvement of several Peruvian primatologists during the extraction of these primates from southeastern Peru, records of the procedures used in these captures were maintained and later published (Encarnacion et al. 1990). It is from their system of multi-compartment traps, designed for the capture of small monkeys, such as *Cebuella* and *Saguinus* spp., that the current protocol on capturing callitrichids derives. There are, however, significant

differences in this basic methodology as applied to the capture and release of wild callitrichids for the study of behavior, given that the observation of the animals subsequent to trapping is of paramount importance to these studies.

III. 1. 3: Capturing Callitrichidae

Capture-and-release programs have been implemented across a wide variety of primate species, for the many distinctive opportunities they afford to overcoming obstacles present in research on free-ranging primate populations (Jolly et al. 2011). Major capture programs for callitrichids have been implemented with several genera (Aragón 2007; Brett et al. 1982; Dietz et al. 1994; Garber & Teaford 1986b; Goldizen et al. 1996; Jolly et al. 2011; Porter et al. 2007; Savage et al. 1993; Suárez 2007; Windfelder 1997a). Long-term monitoring of wild Callitrichidae began as early as 1973 with the capture of *Saguinus oedipus*, (Dawson 1978; Neyman 1977); however, Savage's description of trapping procedures of *Saguinus oedipus* in Colombia some decades later is the only detailed protocol available on trapping and releasing callitrichids in the wild (Savage et al. 1993), while only a couple of protocols are available on darting terrestrial (Sapolsky & Share 1998) and arboreal (Fernandez-Duque 2003) primates.

In the seventies, during the large exportation of primates to research laboratories, *S. fuscicollis* from southeastern Peru were captured and held in a breeding center, which contributed some procedural information to the published literature on callitrichid trapping protocols (Encarnacion et al. 1990). Since these animals were used for breeding and not released post-capture, methods to avoid disturbing habituation to the observer were neither recognized nor implemented. Some general guidelines for primate trapping, however, do exist (Fedigan 2010; Jolly et al. 2011; Powell & Proulx 2003; Sikes & Gannon 2011), but although trapping of primates is common, not every trapping protocol is published (Fedigan 2010). A precise protocol for the capture of wild tamarins is critically absent, and topics addressed here could be relevant to other primate or small mammal trapping protocols as well.

III. 1. 4: Capture Advantages for Callitrichids

Soini and Cóppola (1981), in a seminal study of wild saddleback tamarins in Perú, utilized morphometrics of genitalia and scent glands to assess individual age. The age-structure of a population is critical in long-term studies to evaluate lifespan, behavior, population viability and demographic change. However, this simple yet central piece of information is extremely difficult to acquire for wild callitrichids, primarily because more dominant individuals in a group can influence sexual maturity.

Young adult female callitrichids in their natal groups are thought to undergo reproductive suppression via scent that prevents them from cycling or exhibiting sociosexual behaviors, and thus from reproducing successfully (Savage et al. 1988; Ziegler et al. 1987). In the absence of knowledge of the endocrine profile of each individual, assessments of sexual maturity (and subsequently, age) are often made from physical examinations of the individuals' anatomy. Another marker sometimes used is sociosexual behavior itself, but mating events can be fleeting, and are thus easily missed. Further, captive female cotton top tamarins, once removed from their natal groups, paired with males but exposed to scents from their mothers, exhibit sociosexual behaviors despite an absence of ovarian cyclicity (Savage et al. 1988). This implies that mating behavior alone, even if witnessed, is not an accurate indicator of sexual maturity in callitrichids.

To complicate matters further, both male and female saddleback tamarins that were gonadectomised in a captive study did not alter the frequency of scent marking, but more critically, neither did they change the appearance of their glands significantly (Epple 1982; Epple 1981). The visible portion of the suprapubic scent gland in males and females are made up of both apocrine (secretions are released by budding off of the plasma membrane of the cell) and holocrine (secretions are released by the disintegration of the cell) cells under the dermis

(Zeller et al. 1988). Gonadectomised individuals lost some apocrine function, but visually, their glands appeared unaltered (Epple 1982; Epple 1981). This creates an additional difficulty in assessing age through genital appearance, but it is possible that a morphometric assessment in conjunction with detailing the level of pigmentation visible could shed light on the matter. Ultimately, age evaluations are likely best assessed by evaluation of the dental condition of individuals, calibrated against that of individuals of known age (cf. Phillips-Conroy & Jolly 1988).

III. 1. 5: This Study

The goal of the present study was to evaluate male and female reproductive strategies among two callitrichid species, *Saguinus fuscicollis* and *S. imperator*, using the anatomy of genitalia and scent glands, dental condition, as well as variation in other morphological and behavioral characters. The project thus required the ability to individually identify animals and groups, as well as to establish the age and reproductive status of individuals of both species. Further, it necessitated behavioral observation, requiring as little disturbance of habituation as possible. For such detailed monitoring, individuals need to be identified quickly and consistently, such as upon first glance during scan sampling, which is virtually impossible to achieve in wild callitrichids. Arboreality, sexual monomorphism, and hair-covered faces, in addition to small body size makes individuals difficult to distinguish. This suggested capture and handling of the animals, as these goals fall well within the requirements for such methodology (Sapolsky & Share 1998; Sikes & Gannon 2011).

In this chapter I report the capture and marking methods I used to identify individuals and allow for the collection of morphological and physiological information on two species of callitrichids at CICRA. I discuss the effectiveness and advantages of dual vs. single-animal processing, bait selection, and effects of the program on habituation of these free ranging monkeys. I also discuss critical modifications to traditional trapping strategies that greatly

decrease distress to the animals during and after trapping, while also ensuring the animals' safety.

The primates included in this study, the saddleback tamarin (*Saguinus fuscicollis weddelli*) and the emperor tamarin (*S. imperator subgriscecens*), are diminutive (300 – 600 g), arboreal, sexually monomorphic and morphologically homogenous (Hershkovitz 1977a). While long-term monitoring of *S. f. weddelli* has involved capture-and-release programs, *S. imperator* has rarely been captured, and never before in complete groups for population level monitoring.

III. 2: Capture Methods

III. 2. 1: Project Timeline

This study was conducted across three trapping seasons: November 2009 to August 2010 (Season 1), March to August 2011 (Season 2), and April to August 2012 (Season 3). In 2005, a single group of emperor tamarins (*Saguinus imperator*) at the study site was involved in a trap-and-release program (Aragón 2007). No other capture programs on any primate had been previously attempted at this site. Throughout Season 1, we observed some *Saguinus imperator* feeding at the trap-sites, probably due to previous efforts at trapping them at this site (Aragón 2007). We did not include them in the capture-and-release program due to legal restrictions placed on them for their vulnerable conservation status in Perú. However, in the second field season, we received special permission to include *S. imperator* in our trapping program. All research was conducted with IACUC authorization from the Animal Studies Committee of Washington University in St. Louis and research permits from the Ministry of Agriculture of Peru.

III. 2. 2: Trap Design

The trap designs used in this study were based on models successful in other callitrichid trapping programs, with a few specific modifications. A trap consisted of 6 – 10 contiguous

compartments, each 15 cm wide, 60 cm long, and 30 cm high, made of 1.25-cm galvanized wire mesh and wood stapled together by staple-guns (Fig. III. 1). Plastic zip-ties linked the mesh pieces, and the tails of the zip-ties were snipped off once tight. A push-resistant flap of wire mesh at the top of the entrance to each compartment prevented the doors from being pushed on directly by animals inside. Although previous studies have allowed a 1 cm gap at the top of the door to prevent injuring the tail of the animal, this never occurred with the full-sized doors used in our study. Each trap was examined closely and sharp edges filed down or duct-taped to create a non-abrasive environment for the animals.

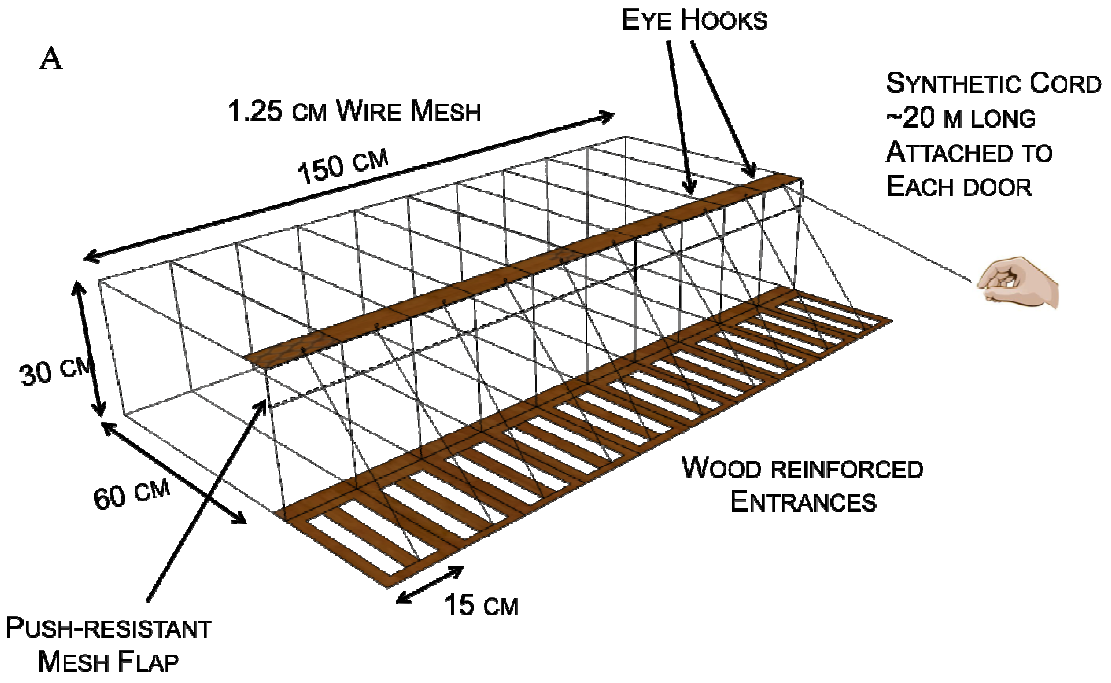


Figure III. 1: Tamarin trap model indicating materials used as well as the dimensions for a 10-compartment trap. The full setup for the door-strings is only shown for a single compartment.

Recovery chambers (roughly the size of a single compartment) were constructed out of wood and wire mesh. Their roofs served as trap-door entrances and were anchored down by placing weights on the cages. The sides and floor inside the chambers were padded with thick towels. A minimum of 6 recovery chambers was used for each group per trapping session. During Seasons 1 and 2, larger recovery cages were utilized in which multiple animals recovered together, but we found having individualized cages for the adults caused the least conflict between animals. The cages were placed together in a grid and covered at all times, allowing for animals to see and touch each other in adjoining chambers.

III. 2. 3: Trap Placement

During Season 1, we placed feeding platforms at 76 sites frequented by *Saguinus fuscicollis*. During Season 2 and 3, only trap-sites successful during Season 1 (*ca*. 6-8 sites) were utilized to recapture and release individuals of both species. However, in order to trap more groups, a few new trap-sites were identified during both Seasons 2 and 3. There are several factors particular to site selection that we found increased the likelihood of habituating groups to baited traps:

1. A tangle of lianas, with at least two running horizontally at *ca*. 1.5 m off the ground to host the trap, and others that provided easy routes from multiple trees towards the trap itself.
2. A path between the trap and the observer, devoid of large trunked trees, but including some vegetative cover that can be manipulated temporarily to allow for a clear passage of the trap's control-strings.
3. A small clearing with flat ground and no vegetation < 30 m of the trap site, for the positioning of a processing station.
4. Close proximity to a resting area for the group in question and low proximity to active fruiting trees at that time.

At selected sites, we hoisted each multi-chambered trap onto a wire-mesh platform, and anchored it to trees with rope at the corners. The traps were tied down at the back to balance the weight of the doors in front. Once positioned, we used thin string attached to the door and threaded through an eye-hook to allow an observer *ca.* 20 m away to operate and shut the doors (Fig. III. 1). We singed the strings at the ends to prevent unraveling, and the color of the string used had no apparent effect on trapping success. We did not use blinds to hide behind during trapping, as the animals were habituated and were not affected by our presence at the trapping site.

III. 2. 4: Incentives to Attract Animals

III. 2. 4. 1: Bait

We did not remove fruits from trees within the study area to use as bait, to avoid disturbing the feeding ecology of other frugivores. We tested two different fruits, *shimbillo* (*Inga* sp.) and *plátanos* or bananas (*Musa* spp.) in this baiting program. Fruits of the *Inga* sp.–small yellow pods with seeds enclosed in sweet white pulp–were collected from plants on the riverbank away from the Conservation Concession. However, we found this bait unsuccessful in that the monkeys searched arboreally for the *Inga* plant once they saw the fruit, making the trap-site less attractive. After exhausting every possible option of bait choice and placement for *ca.* 4 mo in trapping Season 1, we realized that the tamarins at this site were entirely indifferent to bananas, a phenomenon that has occurred in particular primate populations in the Neotropics (Müller & Schildger 1994).

III. 2. 4. 2: Caller Animal

Many studies have overcome this initial aversion to bait by employing a caller or decoy individual, which, when placed next to the trapping site in a similar compartment, produces high success rates in habituating naïve individuals to new fruit in a trap (Buchanan-Smith 1991; Lopez 2011; Terborgh & Goldizen 1985). Our reluctance to use a calling animal, despite its success in the past, reflected concerns for how such an animal would be obtained and for its life

after inclusion in the study. Obtaining a young individual of a particular species could imply participation in the pet trade, either directly or through a local family, and does not guarantee the subsequent rehabilitation of the individual to a life in a free-ranging group of primates. Therefore, the decision to obtain a calling animal was made with some reservation, only to be implemented if the future of the animal could be made secure.

In March 2010, we were fortunate to be loaned a 3-mo old male *Saguinus fuscicollis* from the Taricaya Rehabilitation Center in Puerto Maldonado. The individual, named "Chiky", was quarantined at the Center for 3 weeks before joining the project. He remained with us for 4 months, and was housed in a large cage within the laboratory building at CICRA. We attempted to minimize human handling except to encourage transfer into a traveling carrier each morning. He was fed fresh, local fruit, as well as katydids and grasshoppers. Also, at one trap-site each day from March to July 2010, Chiky was placed in a traveling compartment, which was identical in every way to a single trap compartment, and hung *ca.* 3 feet from the trap, with no direct access provided for the wild tamarins. Chiky was always accompanied by an observer, was fed throughout the session, had a blanket and water within the cage, and remained at a trapping location for *ca.* 5 h each morning. Under adverse weather conditions, he was returned immediately to camp. At the end of his stay, Chiky returned to the Taricaya Rehabilitation Center and he is currently being rehabilitated to join one of the multiple free-ranging captive-raised groups at the Center.

We did not observe any physical interaction between Chiky and any wild tamarins during the study; the wild individuals simply observed him consume the bait in his own carrier, and given the dry season and the scarcity of food, adapted to consuming bananas. Once the initial barrier of unfamiliarity with the bait was crossed (Season 1), bananas were successful as bait for the wild monkeys even without Chiky present (Seasons 2 and 3). No preferences for any specific hybrid banana variety were observed, although large-scale trapping of primates in the 1970s in

Peru did report that some preferences do exist for hybrid *Musa* spp. among the New World primates (Encarnacion et al. 1990).

III. 3: Phases of the Trapping Protocol

III. 3. 1: Baiting Trap-Sites

We chose sites where multiple groups often encountered each other and placed traps in these areas, typically adjacent to resting spots. At each selected trap site, we baited traps in five stages, ranging from placing whole fruit high above the traps to the final stage, with pieces of fruit inside the traps alone (Table III. 1). We baited individual trap sites every morning before 7 am with *ca*. 6 small bananas and monitored them daily by watching the traps in person or through motion-sensing camera traps. Stakeouts of multiple trapsites were conducted each day, during which an observer played long-call vocalizations of both *Saguinus* spp. every 30 min, and recorded responses to the long-call playbacks. If a response call was heard, playbacks of calls of both species were continuously repeated until the group was visible. At this time, we discontinued playbacks and noted direct responses by the group's individuals to the trap and the bait. Stakeouts were conducted from dawn until noon, or from noon until dusk. During a stakeout with Chiky present (Season 1 only), playbacks were used infrequently, as Chiky invariably responded with long-calls to groups in the vicinity, sometimes even before the observer had heard a wild tamarin long-call.

III. 3. 2: The Capture

Once a group was observed to eat reliably at a trap site, with all individuals entering and eating fruit within the trap, capture proceedings were initiated. Both the trap site and the processing station within a 4-person tent, *ca*. 20 m from the trap, were prepared before dawn. Two observers manned the control-strings to the trap, with a minimum two additional assistants within the processing station. All handlers were gloved and masked, and all equipment wiped clean with 70% alcohol before use.

Table III. 1: The five stages of baiting a trap.

Stages	Trap or Platform	Size of Fruit	Placement of Fruit	Minimum Conditions to Upgrade to the Next Stage
Stage I	Platform	Whole fruit	Elevated above the platform (*ca*. 4 m) using bamboo poles	Animals must try the bananas and/or venture onto the platform
Stage II	Trap	Whole fruit, small pieces	Whole fruit remain elevated, but small fruit are placed on the trap's roof and doors	Animals must pick up pieces off the trap, and be spending time feeding at the whole fruit
Stage III	Trap	Small pieces	On trap doors and roof	Animals must descend to feed from the trap, and venture onto the doors
Stage IV	Trap	Small pieces	On doors and inside the trap, but not on the roof	Animals must venture inside the trap compartments, but it's alright if they only grab the fruit and leave to eat it in the trees
Stage V	Trap	Large pieces	Inside the trap only	Animals must remain within the compartments eating the fruit without removing it from the trap itself. At this stage, if all animals in the group are entering the trap, they are ready for capture.

These stages occur before capture can be attempted, and are described in terms of bait placement as well as the minimum conditions that must be met in order to move on to the next stage.

Durations for each of the stages depend on the level of habituation of the group to observers, the trap and the fruit.

Overall success is observed to be highest in the dry season with groups that are being newly introduced to this fruit.

Where possible, we trapped full groups before 10 am so that the last processed animal to recover (*ca.* 1.5 h after the final anesthetic dose) could be released together with its group at least 1.5 h before dusk. When a single animal remained outside the traps, we did not wait long for it to enter the trap, due to increased stress on those within the trap. The age-class of the excluded animal determined our next steps. A juvenile or younger animal was never left alone and another animal would be released to keep it company. If a mature individual were excluded, we proceeded with the trapping protocol by lowering the trap, securing the doors, cutting the control-strings loose, and covering the trap with a tarpaulin. Animals always remained near the area until their groups were released.

III. 3. 3: Anesthetization Procedures

Protocols when described in the literature depict a simple system of anesthetization – although a whole group is captured at once, only a single animal is anesthetized at a time, while the remaining animals remain in the trap (Savage et al. 1993). At the start of Season 1, during the processing of the first two groups of *Saguinus fuscicollis weddelli*, we followed this procedure, hereafter referred to as the Single-Phase or P1 anesthetization process. We observed a high rate of self-inflicted injuries in one of the groups (SF2) that underwent the P1 process while individuals waited in the original trap. Subsequently, for all other groups, we used a Two-Phase or P2 anesthetization procedure, where all animals trapped were anesthetized first and vitals collected (termed initial processing), and then a second time for all remaining data to be collected (complete processing), spending the time in between within a recovery chamber. In this system, complete processing was only initiated once initial processing was achieved for all captured animals in the group. Further, the anesthetic doses were minimal during initial processing, and higher and more weight-specific during complete processing.

III. 3. 3. 1: Choice of Drug

The choice of a drug to use on animals in the wild depends on a number of factors, including its mode of administration, safety, side effects, availability and dosage. For this project, the drug needed to be stable at room temperature, available locally, and have demonstrated use in tamarins in the past. Since the initial dose is administered to an animal whose precise weight is yet unknown, the drug should have a wide safety margin eliminating the risk of administering an overdose. The most commonly used drugs for field immobilisations of primates are dissociative anesthetics, or cyclohexamines, such as ketamine hydrochloride and tiletamine hydrochloride (Ancrenaz et al. 2003). They render an animal unresponsive while maintaining reflexes, thermoregulation and blood pressure (Sapolsky & Share 1998). We chose to use ketamine-hydrochloride at a dose of 10-20 mg/Kg, which is within the range of doses used on tamarins previously (Ancrenaz et al. 2003; Savage et al. 1993), administered intramuscularly into the thigh.

III. 3. 3. 2: Drug Side Effects, Possible Complications, and Solutions

All anesthesia effects are accelerated in smaller primates, and so a 400-g tamarin, with a high metabolic rate, will metabolize a given anesthetic faster than the average primate (Ancrenaz et al. 2003; Kreeger 2007). During recovery from ketamine, tamarins display increased muscle tension and are sensitive to stimuli, appearing in a trance-like state with locomotor difficulties (Ancrenaz et al. 2003). They also display increased salivation during induction, which is a risk to respiration and can be countered with atropine at 0.02-0.06 mg/Kg (Ancrenaz et al. 2003). Finally, temperature spikes are common upon the administration of the drug (Ancrenaz et al. 2003; Sapolsky & Share 1998), especially in tropical conditions, and so the animal is kept cool by misting water over the abdomen and using fans to encourage evaporation. A smoother induction is possible with the coupling of ketamine with a tranquiliser such as xylazine (Ancrenaz et al. 2003; Kreeger 2007; Sapolsky & Share 1998). However, tranquilisers

function by depressing the central nervous system, causing slower heart rates and breathing (Ancrenaz et al. 2003), and can cause vomiting in primates (Kreeger 2007). Having worked with solely ketamine hydrochloride during this project, the risks associated with xylazine seem to outweigh the benefit of a smoother anesthesia, particularly in field conditions where surgical plane anesthesia is not necessary (Green et al. 1981); however, tiletamine hydrochloride (sold as Telazol – including the tranquiliser zolazepam) has been used successfully on primates and we would be willing to consider it in the future (Agoramoorthy & Rudran 1994; Melo et al. 2012; Sapolsky & Share 1998).

The American Medicinal Drug Use Clarification Act (AMDUCA) specifies withdrawal times for all drugs used on animals, which it defines as the time after the administration of the drug that the animals is considered safe for human consumption. Ketamine hydrochloride has a withdrawal time of three days, Telazol lasts for 14 days, and xylazine effects linger in the animal for 30 days after use (WAFWA 2010). There have also been some concerns that ketamine hydrochloride alters serological levels of adrenocorticoids in animals, with certain systems more severely affected than others (Castro et al. 1981; Gossett et al. 2009; Walker et al. 1987), which would be important to consider when obtaining blood for endocrine analyses; this is not a concern in this particular project at this time but could conceivably be affected by the two-step anesthetization protocol.

III. 3. 4: Processing Methods

In addition to these two general strategies, we also attempted two different methods of processing: (1) a single individual was processed at a time, as is common in the literature (Individual Processing), and (2) a pair of individuals was processed simultaneously (Dual Processing). By Season 2, we shifted to processing all animals singly and so, *S. imperator*, which was only captured for the first time in Season 2, never underwent dual processing.

III. 3. 4. 1: Initial Processing

In P2 anesthetization, we administered a single low dose of anesthetic (Ketamine hydrochloride) to each animal, through the mesh of the trap after lightly pressing the animal against the mesh. Those too young to travel independently were not anesthetized. The animal was then transferred to the processing tent for basic monitoring, including recording sex and current or previous injuries. We also measured body temperature, respiratory rate and palpebral responses at 2-minute intervals for the first ten minutes, and every ten minutes after. Since we aimed to trap whole groups at a time, we could not avoid processing animals through the middle of the day when temperature stress is high. Ketamine is known to rapidly raise body temperature, which we countered with spray bottles with cool water and fans to lower body temperatures to ~ 100 °F. While they waited for processing, we transferred each monkey to a mesh bag for holding within the recovery chambers. We found these bags an effective restraint and protective measure for the animals, allowing them to breathe and move, but not be completely mobile. The last animal anesthetized received a larger dose, appropriate for its weight, and passed directly into complete processing without spending time in the recovery chamber.

III. 3. 4. 2: Complete Processing

During this period, data on dentition, body weight, limb measurements, health, and injuries were recorded for each animal. Approximately 300 μL of blood was drawn for genetic screening from either the saphenous or femoral vein, which is well within limits prescribed for mammals (≤ 1.5% of body mass) (Sikes & Gannon 2011), as well as other callitrichid studies (e.g. Telxeira et al. 2012). Each individual was also marked in three separate ways: a permanent identification via a Home Again microchip inserted between the shoulder blades, bleached rings around the tail (for a mean time of 30.9 ±13.7 (sd) mins), and a tricolor-beaded collar around the neck (Agoramoorthy & Rudran 1994; Araújo et al. 2008; Buchanan-Smith 1991) (Fig. 2). We modified the typical three-bead system (denoting group, sex and individual) (Garber & Teaford

1986b) to include two sets of such beads, one hanging in front and one behind, so that individuals were recognizable when their backs faced the observer. Beaded collars were constructed in two sections, each containing a set of three plastic beads hanging off a length of beaded chain; subsequently the two pieces of chain were attached to each other with clasps. The lengths of chain used are as follows (parentheses indicate the number of beads along each piece of chain on a single collar): 2.9 cm (10 beads) for adults and 2.3 cm (8 beads) for infant *S. fuscicollis* and 3.4 cm (12 beads) for adults and 2.9 cm (10 beads) for infant *S. imperator*.

During Seasons 1 and 3, an individual in each tagged group of tamarins was given a radio collar (Season 1: Telonics, CHP-6P, weight ~4 g, lifespan: 3.5 mo; Season 3: Wildlife Materials, SOM-2190, weight ~ 8 g, lifespan: 9.0 mo) that weighed less than 3% of average weight of an adult tamarin, well within the recommended limits of <5% of body weight for mammals (Cuthill 1991). A ball and chain collar system was used to mount the telemeters to the animals; fortunately, although the animals chewed the long antennae almost immediately, there was no loss of signal from the machines themselves. No collars were deployed in Season 2. In Season 1, we avoided radio telemetry of lactating mothers, and chose young females instead; however, these females were highly likely to disperse from groups. In Season 3, therefore, radio collars were placed on dominant, breeding females within each group.

Figure III. 2: Marked individuals of both tamarin species post-capture. A1shows bleached tails and beaded collars on *Saguinus fuscicollis*. B1 shows a beaded collar on *Saguinus imperator*.

III. 3. 5: The Release

After processing was completed, each monkey's tail was washed with water and hypoallergenic shampoo to remove traces of bleach, and the animal was thoroughly dried. We then placed the animal into a recovery chamber without a mesh bag. All animals remained in these chambers, with fruit and water provided, until each exhibited coordinated movement and processing of all animals in the group was completed. Holding times ranged from 47 min for animals processed first, to *ca*. 6.8 h for animals processed last. Each animal spent an average of 3.5 h in the recovery chamber after the last shot of anesthetic was received.

Animals were intentionally housed together in the recovery cages, taking care to put infants with mothers, and splitting up the sexes where possible. During the release, we placed the recovery chambers within 10 m of the trap-site used for capture after the trap was replaced on the mesh platform and re-baited. We then carefully released the full group at one time, often noticing that they approached the traps for fruit immediately. As processing typically took up a large part of the day, groups tended to then retreat to sleep sites after release. However, we only followed the released monkeys to verify that all group members were reunited, and then withdrew to minimize further stress on the groups. All trap-sites were baited for at least 2 – 4 days after trapping occurred, allowing the animals to return to the site and feed if they chose.

III. 4: Evaluation of the Modified Trapping Protocol

III. 4. 1: Trapping Success

I measured trapping success by the number of groups and the total number of individuals trapped per species during this project. In total, we conducted 184 baiting trials across 79 sites. Each trial consisted of a two-week intensive baiting strategy at a site, involving individual monitoring and vocalization playbacks every morning for at least 7 of the 14 days. Bi-monthly percent trapping success, or the percent of baited trap-sites at which animals were trapped successfully per 2-week trial, was then calculated across all three trapping seasons, including the period during which the caller animal was present at CICRA (March – July 2010) (Figure III. 3).

III. 4. 2: Effect of Protocol Modifications

In order to increase the safety of the animals, and the efficiency of the protocol, we instituted two major modifications to the protocol in Season 1. First, we processed some animals in pairs, and second, we introduced a two-phase anesthetization protocol for a portion of the trapping instances. Largely driven by the goal of minimizing time spent within the trap while not under an anesthetic, which successfully eliminated self-inflicted injuries during trapping, the obvious concern arose that these modifications could worsen overall trapping efficiency. I evaluated this possibility by comparing two measures, the total dose of anesthetic received and the time taken for complete processing, between animals who underwent either single vs. dual processing, or one vs. two-phase anesthetization. For both tests, we ensured only trapping instances involving the same number of tasks were included in the analyses. I used Mann Whitney two-tailed U-tests at an alpha-level of 0.05 to compare these types of processing.

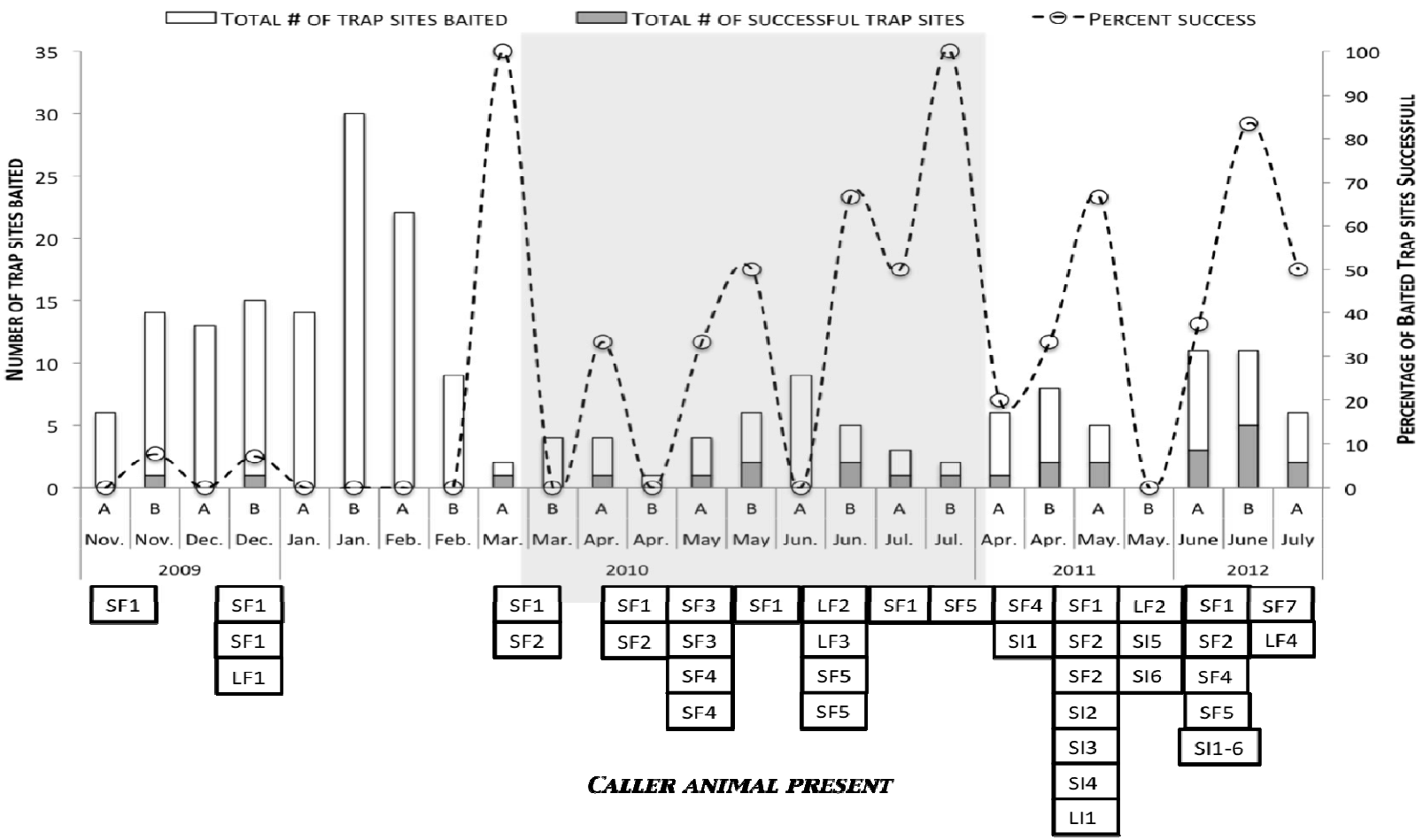


Figure III. 3. Trapping success across the study duration. A single success is defined as the successful capture of a group or part of a group on a particular day. Each month is divided into two halves. The grey shaded section indicates the presence of the caller animal. Boxes below indicate trapping of groups or lone individuals and are coded as SF = *Saguinus fuscicollis*, LF = Lone individual of *S. fuscicollis,* SI = *S. imperator*, LI = Lone individual of *S. imperator*.

It is important to note here that processing times are dependent on the data collected and the team of observers used, slightly different each season, rather than the identity or species of the subjects processed. As such, I analyze trapping efficiency by season, and within each season, treat all trapping instances where the same tasks were performed as comparable to each other. Since the identity of the animals trapped does not affect processing time, resampling methods are deemed unnecessary in these analyses. Due to the complex nature of processing, in some cases data were either incorrectly collected or not collected at all for an individual, and these instances have been excluded from the dataset.

III. 4. 3: Assessment of Habituation

I also evaluated whether the tamarins regard the trapping experience negatively by recording their behavior towards the trap and the observer, before and after capture. Groups were regarded as habituated to human observers if they could be followed for at least 5 hours continuously. Groups were classified habituated to the trap if they returned to the trap post-capture. However, since we did not attempt to follow groups for a few days after trapping them, we could not be sure of the exact time taken to approach the trap post-capture in all cases.

III. 5: Results: Evaluation of the Trapping Protocol

III. 5. 1: Trapping Success

Over the three field seasons, 7 groups of *Saguinus fuscicollis* and 6 groups of *S. imperator* were successfully included in the trapping program. In addition, several lone individuals of both species were also tagged, resulting in a total of 57 *Saguinus fuscicollis* and 36 *S. imperator* in the trapping program.

The tamarins did not eat bananas for approximately 80% of baiting trials in Season 1. Subsequently, a caller animal was introduced, causing a dramatic increase in bi-monthly percent trapping success. The notable exception to this is the trapping success of November and December of 2009, where a single group of *Saguinus fuscicollis* (SF1) and a lone male (LF1)

were trapped without further habituation. Other than these individuals, however, no other groups of *S. fuscicollis* were observed feeding at trap-sites until the introduction of the caller animal.

In Season 2, even though no caller animal was used, trapping success remained high, with an ~ 90% reduction in the number of baiting trials necessary for trapping from Season 1 (152 segments) to Season 2 (14 segments) (Fig. III. 3). Season 3 displayed a similar trend, with only 18 baiting segments used with a high of *ca*. 85% trapping success in June 2012 over 8 trap sites. The most reasonable explanation is that the caller animal increased the effectiveness of the baiting strategy in Season 1, which resulted in fewer baiting trials necessary for recapture in subsequent seasons. In fact, habituated groups feeding at the sites seemed to encourage naïve groups to try the fruit. It was not necessary to employ a caller animal for Seasons 2 or 3 due to the apparent transfer of knowledge of the palatability of bait items from habituated to naïve groups.

III. 5. 2: Processing Methods

During initial trapping attempts, we followed a Single-Phase anesthetization procedure as described in the literature and left individuals in the trapping apparatus while others were processed (Savage et al. 1993). With this strategy, we trapped group SF1, which was the most habituated group with a core home range centered directly at camp, in November and December 2009. We processed these animals within the laboratory, observing no injuries to animals from remaining in the trap without anesthesia during processing of other group members. However, when group SF2, with a home range away from the field station, was trapped in March 2010 using the same procedure, we observed several self-inflicted wounds on the animals that waited within the traps. These included scraped brows and muzzles from attempting to break through the wire mesh. As we are certain the animals were not injured during initial capture, it seems that the animals' distress at remaining in a trap for extended periods of time was so great that

they injured themselves and each other. After this experience, we developed the Two-Phase anesthetization procedure that was subsequently used on all groups, including SF2 during all three trapping Seasons. With this method, each tamarin is instantly anesthetized and transferred to a mesh bag held within a padded recovery chamber, which reduces stress during the trapping process and effectively prevented any further injuries to the animals.

We found no significant differences between mean processing times or anesthetic doses received by animals that underwent single vs. paired animal processing for *Saguinus fuscicollis* in Season 1 (two-tailed Mann Whitney U-test, $\alpha = 0.05$) (Table III. 2). However, we observed that for a team of four observers, the processing of two animals simultaneously increased the number of variables that needed to be recorded, and data omissions were increasingly common. Our preference since was to work with single animals at a time.

Table III. 2: Results of Mann-Whitney U tests comparing two processing and anesthetization methods tested on *Saguinus fuscicollis* in Season 1.
All mean values presented as mean ± standard deviation. Values in parentheses indicate sample size of trapping instances.
"+" indicates that the total anesthetic dosage here excludes the initial shot received during initial processing.
Note: Only values for animals with weights > 250 g are used for analyses in order to exclude infants and juveniles from biasing the processing times.

	Processing Methods			Anesthetization Procedures		
	Single	Paired	*p*	One-Phase	Two-Phase	*p*
Mean Total Processing Time (min)	79 ± 41 (15)	82 ± 35 (15)	> 0.05	76 ± 41 (21)	93 ± 25 (9)	> 0.05
Mean Total Anesthetic Dose (mg/ Kg)	24 ± 9 (16)	22 ± 9 (20)	> 0.05	21 ± 9 (27)	22 ± 8 (9)+	> 0.05

Table III. 3: A comparison of processing times and anesthetic doses across the three trapping season for *Saguinus fuscicollis* and *S. imperator*

All mean values presented as mean ± standard deviation. Values in parentheses indicate sample size of trapping instances.
"+" indicates that the values here represent the total anesthetic dose received, as opposed to the values in Seasons 2 and 3, which exclude the initial dose received by the animals from the total dosage due to two-phase processing.

	Season 1 Nov. 2009 – Aug. 2010	Season 2 Mar.– Aug. 2010		Season 3 Mar. – Aug. 2011	
	SFUS	SFUS	SIMP	SFUS	SIMP
Mean Total Processing Time (min)	77 ± 40 (32)	38 ± 5 (9)	41 ± 6 (24)	52 ± 13 (31)	59 ± 11 (20)
Mean Anesthetic Dose (mg/ Kg)	22 ± 9 (39)+	9 ± 3 (9)	10 ± 4 (26)	9 ± 4 (31)	12 ± 6 (21)
Mean Weight (g)	387 ± 59 (39)	402 ±24 (9)	530 ± 109 (26)	371 ± 46 (31)	451 ± 102 (21)

Note: Only values for animals with weights > 250 g are used for analyses in order to exclude infants and juveniles from biasing the processing times. SFUS: *Saguinus fuscicollis*; SIMP: *Saguinus imperator*

When comparing mean processing times between animals that underwent one-phase and two-phase anesthetization procedures, once more, there was no significant delays to processing due to the change in procedure (Table III. 3). Further, when I compared the total anesthetic dose received during one-phase processing with the anesthetic dose for complete processing during the two-phase method (total anesthetic dose save for the initial anesthetic dose), I found no significant increase in doses necessary for the utilization of the two-phase method.

Finally, I also found that values for mean total processing time and mean anesthetic dose dropped in Seasons 2 and 3, resulting from the streamlining of processing of single animals with more experienced teams of observers. The average anesthetic doses received by both tamarin species in Seasons 2 and 3 are well below that utilized in other studies (ca. 25 mg/Kg by Savage et al. 1993), and processing of each animal occurs in just under an hour or average. No significant self-inflicted injuries were observed during these two seasons.

III. 5. 3: Equipment List

Another result of our trapping program was the identification of the most useful and currently available equipment for trap construction, marking, processing and data collection. Therefore, we present here an updated list of products we used in successful tamarin trapping (Table III. 4). All attempts were made to use biodegradable, hypoallergenic, non-electric and waterproof products wherever possible.

Table III. 4: Products chosen for specific tasks, including their source, specifications and the reason for choosing them.

Product Name	Specifications	Purpose	Reasoning
Trapping			
Eureka Tetragon 9 4-person tent	Green, 9' x 9' floor dimensions, single door	For insect-free working conditions during processing	A green tent is less visible, sturdy, insect-repellent. Holds 4 people.
Hardware cloth	½" galvanized steel mesh	Floor, roof, sides and doors of the trap	The spacing is smaller than tamarin foot. Galvanized metal won't rust quickly, spray paint to extend life.
Altec Lansing iM-237 Orbit Speaker	None	Playback of vocalizations to attract tamarins	Light, small, cheap, excellent battery life and relatively water-resistant.
Staple Gun	Aero Fastner Red Gun with ¼" leg x 3/8" crown T50 steel staples	To attach mesh to wood for trap construction	Non-electric, light, manually operated. Zipties used to attach mesh to mesh.
Basic Monitoring			
Pesola Medio-line Spring Scale	Forestry Suppliers FS 93015, 1000g scale	Accurately weigh animals in a cloth bag	Waterproof, affordable and accurate.
Mesh bags	1'x1' white mesh laundry bags	Semi-restricted space for animal after initial processing	Zippers break easily, so rubberband the bag shut.
Thermometers			
Marking and Data Collection			
Bleach	Clairol BW2 powder bleach	Temporary marking of tail hair	Gentle on skin, fast acting, no heat required.
Developer	40	Mixed with bleach	Needs to be airtight as it does get oxidized.
HomeAgain Avid Microchips and Reader	Microchip ID Systems	Permanent identification tag.	Easy to find in America, hard to replace outside the country where chips follow ISO standards. Match microchip reader to chip.
Neiko Digital Caliper	Stainless steel, 12", LCD display	Morphometrics	Easily read, good battery-life, accurate.

III. 5. 4: Habituation

For groups that were recaptured, multiple trapping events and their effects on behavior were recorded (Tables III. 5 and III. 6). All groups were completely habituated to the presence of the observer at the baited traps before being trapped. After trapping, we observed groups feeding in the traps used to capture them in all cases, with only one exception – Group SF2. Some groups even returned immediately after capture to the traps to feed. Only two groups, SF2 and SF5, exhibited a change in attitude towards the observer, becoming extremely difficult to track and follow post-capture, but these effects did not persist from trapping season to season. The number of new immigrants in a group was negatively impacted the ease with which a previously habituated group could be followed by an observer.

Table III. 5: Group behavior post-capture across all trapping seasons for *Saguinus fuscicollis*.

Group	Trapping Season	Trapping Event	Number of Individuals Processed	Group Size	Revisited Trap?	Habituated to Observer?
LF1	I	1	1	1	Y	Y
LF2	I	1	1	1	Y	Y
LF2	II	2	1	1	Y	Y
LF3	I	1	1	1	Y	Y
LF4	III	1	1	1	Y	Y
SF1	I	1	2	5	Y	Y
SF1	I	2	3	5	Y	Y
SF1	I	3	5	5	Y	Y
SF1	I	4	3	5	Y	Y
SF1	I	5	2	5	Y	Y
SF1	I	6	4	5	Y	Y
SF1	I	7	4	5	Y	Y
SF1	II	8	4	4	Y	Y
SF1	III	9	6	6	Y	Y
SF2	I	1	4	4	N[a]	N[a]
SF2	II	2	2	5	Y	Y
SF2	II	3	3	5	Y	Y
SF2	III	4	4	5	Y	N[b]
SF3	I	1	5	6	Y	Y

Table III. 5. ***Continued***

Group	Trapping Season	Trapping Event	Number of Individuals Processed	Group Size	Revisited Trap?	Habituated to Observer?
SF3	I	2	1	6	Y	Y
SF4	I	1	5	6	Y	Y
SF4	I	2	1	6	Y	Y
SF4	II	3	5	6	Y	Y
SF4	III	4	7	7	Y	Y
SF5	I	1	3	5	Y	Y
SF5	I	2	5	5	Y	N[b]
SF5	III	3	8	9	Y	Y
SF6	I	1	3	3	YS	Y
SF7	III	1	7	7	YS	Y

[a] Did not revisit trap that year, but did the next year. Fled from observer after use of single-phase anesthetization protocol.

[b] One individual in this group seems to be averse to the observer, but not to the trap.

Y = Yes; N = No; YS = revisited the trap immediately after release; I = Trapping Season 1; II = Trapping Season 2. SF = *Saguinus fuscicollis*, LF = Lone individual of *S. fuscicollis*, SI = *S. imperator*, LI = Lone individual of *S. imperator*.

Table III. 6: Group behavior post-capture across all trapping seasons for *Saguinus imperator*.

Group	Trapping Season	Trapping Event	Number of Individuals Processed	Group Size	Revisited Trap?	Habituated to Observer?
SI1	II	1	3	3	Y	Y
SI1	III	2	5	5	Y	Y
SI2	II	1	6	6	YS	Y
SI2	III	2	5	6	Y	Y
SI3	II	1	3	4	Y	Y
SI3	III	2	6	6	YS	Y
SI4	II	1	6	6	Y	Y
SI4	III	2	2	3	Y	Y
SI5	II	1	5	6	Y	Y
SI5	III	2	3	3	YS	Y
SI6	II	1	4	4	Y	Y
LI1	II	1	1	1	YS	Y
LI2	III	1	1	1	YS	Y

Y = Yes; N = No; YS = revisited the trap immediately after release; I = Trapping Season 1; II = Trapping Season 2. SF = *Saguinus fuscicollis*, LF = Lone individual of *S. fuscicollis*, SI = *S. imperator*, LI = Lone individual of *S. imperator*.

III. 6: Discussion and Conclusions

We successfully captured and released 13 groups of saddleback and emperor tamarins from 2009 to 2012 using a multi-compartment trap. Although rifles and blowpipes have been used to deliver an anesthetic to other free-ranging New World Monkey species (Fernandez-Duque 2003; Glander et al. 1991), the miniature size of tamarins precludes such methods due to the high possibility of their sustaining major injuries from the force of the darts themselves. Darting in general has been deemed to be more hazardous than trapping to the animal, less productive, and more likely to inhibit post-capture habituation to the observer (Cunningham & Setchell 2012; Jolly et al. 2011). We found the trapping method very effective with this population of free-ranging tamarins. Initially, we had to overcome the tamarins' natural unfamiliarity with bananas as food. The introduction of a caller animal for 4 months during the first trapping season significantly increased the effectiveness of bananas as bait items. Bananas (*Musa* spp.) served as bait successfully for two subsequent trapping seasons. We have observed *Cebus*, *Callicebus* and *Callimico* feeding at the traps; however, only *Callimico* can actually enter a trap due to the small size of the compartments. Our camera traps recorded evidence of tayras (*Eira barbara*), nocturnal marsupials and rodents showing interest in the trap sites as well.

We observed that placing traps in areas of home range overlap between habituated and unhabituated groups greatly increased the likelihood of the less-habituated group eventually feeding at the site. We believe the inhibitions of naïve groups are lowered after observing habituated groups feed safely at a trap. We also modified the trap structure to include a few features that increased the viability of our trapping strategy. First, the use of zip-ties allowed us to attach mesh pieces together without wood, resulting in a lightweight trap that was structurally sound. The push-resistant mesh flap at the top of the cage resulted in fewer escapes during capture, allowing us to process entire groups without individual escapes. The final trap structure was free of abrasive surfaces, nails or sharp edges, and was unlikely to cause the animals harm. Painstaking efforts were made to position traps at locations compatible with

tamarin ecology. For example, trap sites were selected according to features of the vegetation at the site that increased the accessibility to the trap for a small primate.

We found that placement of bunches of unripe bananas elevated by bamboo poles to be very effective in habituation, as the fruit ripened over some days, mimicking natural conditions. Typically a tamarin group showed no interest in the baited trap, spending time sniffing and touching only the elevated fruit. Upon observing either the caller animal or other free-ranging tamarins eat at the site, the group typically fed on the elevated fruit first. Younger individuals tended to be the first to approach the traps themselves, often eating fruit on top of the trap alongside other habituated tamarin groups. These individuals, however, took much longer to realize that the trap's doors opened on one side, providing easy access to the food inside. Eventually adults from the group ventured onto the trap, stealing pieces of fruit to eat in the safety of the trees. Finally, we provided only whole fruit inside the trap compartments, which effectively encouraged the animals to eat the bait inside the trap.

We observed that increased time spent in traps, specifically while other group members were being processed in single-phase processing, resulted in a high incidence of self-inflicted facial injuries due to efforts at escaping the trap. Other than for a single group early in the first trapping season, this strategy was never repeated. Instead, we developed a novel method (two-phase processing) that required the anesthetization of all individuals in the trap with the minimum amount of anesthetic possible, after which they were transferred into padded recovery cages where they awaited processing. Although no significant difference in anesthetic doses applied was observed between single and two-phase anesthetization protocols, the absence of injuries occurring with two-phase anesthetization makes it a highly preferable method of trapping for our purposes. However, should we endeavor to measure serological values in this species, we would have to collect blood during initial processing to avoid the dampening effects of ketamine hydrochloride on adrenocorticoid secretions (Castro et al. 1981; Walker et al. 1987).

We assigned individual identifications to each monkey captured using beaded collars, as well as bleached tail rings (Fig. 2). We also modified the standard beaded collar protocol to add a second set of beads so animals could be identified when facing away from the observer. Although initial interest in the collar was observed to be high, after a few days, the individual and other group members ignored the collars. The use of a ball and chain collar on both the beaded and radio collars allowed us to easily manipulate collar sizes, which were estimated based on experience, allowing room for growth. The youngest individual collared was 4 months old, and recapture indicated no effect of collars on the neck and hair despite growth. This is not easy to achieve, as collars have been known to cause injury to *Callicebus* in other trapping programs (Müller & Schildger 1994), and thus our collar sizes are highly recommended for standard usage among animals of this size (note even the small weight difference between the two species changes the collar sizes).

One of the advantages of a capture-and-release program is the ability to place radio collars on individuals so that groups can subsequently be located and tracked. Radio collar options for callitrichids are severely limited; their diminutive sizes restrict the weight of a collar that can be safely carried by a miniature primate. It is impossible, then, to take advantage of new technology such as in-built GPS or programmed drop-offs. We did not test radio collars anchored by backpacks, as it is possible that the backpack units could hinder an individual's ability to carry infants, a common and necessary behavior in a cooperatively breeding primate.

We used diluted bleach to successfully bleach ringed patterns into the tails of both species of tamarin, with much more success in the dark saddleback tamarins than with the emperor tamarins. Infant tamarins were bleached very lightly in different patterns across their bodies, as their tails were too thin to be easily visible. These bleached sections on adult tails routinely molted along with the rest of the pelage within 3 months of application, fading rapidly in the last month. No adverse effects on hair growth were observed in any recaptured individual.

The microchips used to mark individuals were reliably detected upon recapture in all individuals, having remained for 3 years in some individuals. Despite the size of the chip, the highly beveled needle forms an effective delivery system causing no bleeding whatsoever when inserted subcutaneously between the scapulae. Once released, animals were never observed to detect its insertion or attempt to remove it; however, 2 chips have been undetectable over all animals caught in the three years.

Although we attempted to capture the entire group during each trapping session, we did not want to wait too long for remaining individuals to enter the trap as this increased time spent in the trap by initial captured group members, which is correlated with increases in self-inflicted injuries. This meant that there were occasions in which trapped groups had to be reunited with the remaining individuals in the group. During processing, these non-trapped individuals remained close, often feeding in the trap that we had replaced at the trapping site. Therefore, processed animals were never observed to encounter difficulty in locating their group members. No mortalities associated directly with the trapping protocol were observed in this study; however, one young female who was captured and released successfully in Season II subsequently passed away 2 hours after fully recovering from the first small dose of anesthetic when trapped in Season III. Her poor body condition post-mortem also revealed a possibly history of disease.

III. 6. 1: Are Tamarins Afraid of the Trap After Capture?

Once a primate has undergone a negative experience associated with a foraging endeavor, it could be expected to form a negative association with that particular stimulus or setting, which jeopardizes the feasibility of capture-and-release programs conducted in conjunction with behavioral sampling. In some studies, trapping methods have been used that involve automatic traps and single-animal captures, which do not allow for habituation post-trapping. A survey of 120 studies involving trapping of ~65 species of free-ranging primates revealed, however, that a

well-planned study does not cause habituated animals to change their behavior towards observers (Jolly & Phillips-Conroy 1993). Since one of the primary fears of implementing a capture-and-release program in this setting was that it would disrupt tamarin habituation, I evaluated some measures of the degree of habituation before and after trapping sessions. Although there are several ways to measure the extent to which primates are habituated to an observer, such as the distance between the observer and the primate, or the extent of contact time with the animals, I used qualitative behavioral indicators of familiarity to an observer, such as vocalization cues and lack of acknowledgement of the observer's presence, to understand the attitude of a group to being followed post-trapping.

Taking a more subjective approach, we report that in all 42 trapping sessions conducted over three trapping seasons, we observed all groups, with only one exception, return to the trap site to feed within days following capture. Groups SF1 and SF2 were the only groups on which the single-phase anesthetic protocol was used. Group SF1, which was highly habituated to observers and to the bait before the use of the caller monkey, did not react negatively to spending time within the trap. The individuals in SF2, however, were less habituated to the bait and suffered self-inflicted injuries due to time spent in the trap. We believe that this delay in providing an anesthetic resulted in a clear memory of the moments in the trap, even if the processing itself was not clearly recalled, which explains their reluctance to approach the trap later that year. It was this experience that prompted us to permanently shift to the two-phase anesthetic protocol, which has been successful in all subsequent trapping endeavors with this population.

Only one other group, SF5, showed any signs of negativity towards the observer post-capture. When we first trapped three of the five individuals in the group, a single female exhibited an unusual reaction to the trapping process. Even before she was anesthetized for the first time, she was entirely limp and docile. A small puncture mark on her leg discovered during

initial processing indicated the possibility of a powerful insect sting, the effects of which rendered her weak. After processing, despite waiting several hours, she remained docile and awake but unmoving. We released her group but kept her under supervision. She had a good appetite but only two days later, when she developed alarm responses to stimuli such as light or sound, and was moving in her cage, we released her and she was reunited with her group. One month later, we had the opportunity to capture the remaining individuals in the group, and she entered the trap and to our surprise, refused to exit. We eventually were forced to recapture the entire group. Not intending to cause her stress, we did not anesthetize her but instead, transferred her directly to a recovery cage where she spent the morning while the rest of the group was processed. It was a few days after this second trapping that we noticed a change in the group's behavior. The female in question trilled and alarm-called continuously at the sight of an observer, making it impossible to collect normative behavioral data on the group. This behavior continued until the end of season 2, when the group began to eat freely at traps despite her presence in the group and allowed us to make full-day follows. However, by this time, it was too late in the season to recapture the group. Such idiosyncratic reactions to the anesthetic, or the trapping procedure, particular to certain individuals, have been noted by Sapolsky in his extensive work with darting baboons (1998). He recommends being sensitive to these differences as particular individuals can, upon repeated recapture, consistently display specific reactions to the process that others do not.

In the vast majority of cases, the recapturing of a group does not have a negative effect on a group's behavior (see examples in Tables III. 5 and III. 6). Neither does the incomplete capture of a group necessarily affect post-capture behavior, as evidenced by this study. It seems probable that the lack of anesthetic provided to the female in question during her wait for the group left her with a clear recollection of the trapping process. Ketamine is known to cause low-anxiety states with temporary short-term memory loss in mammals (Sapolsky & Share 1998), which did not occur in her case. Her prominent standing in the group (she gave birth to infants

in Season 2) may also have had an influence on the reaction of the group as a whole. During Season 3, all eight individuals in her group were captured but she once more refused to enter the trap. However, she did not react negatively to observers and her group was subsequently followed without any difficulty for the entirety of the Season.

III. 6. 2: Conclusions

There are many ethical concerns that arise with regard to implementation of capture-and-release programs on free-ranging populations of primates. Habituated primates respond well to these programs, but there are still risks to be considered. While these doubts are plausible, experience demonstrates that capture is not an inevitably traumatic event for an animal. As times change, we should continually re-assess trapping strategies and make use of new technology that alleviates stress to study subjects. The data on health and physiology accumulated from capture-and-release programs has revolutionized our perspectives of both captive and wild animals, but at no time must the acquisition of data be given higher priority than the health and safety of the animal. To determine the success of a trapping protocol, one can monitor the time spent by the animals in traps or under anesthesia, as well as their post-capture behavior. If behavioral monitoring were required for all capture-and-release programs, the likely result would be the further improvement of trapping protocols.

III. 7: Chapter Summary

1. A caller animal caused a dramatic increase in trapping success but it was not necessary to include one in subsequent field seasons as the behavior (of feeding at baited trap sites) propagated through the population.

2. A single-step processing method causes injuries, so we propose a two-step anesthetization process which shows no significant delays in processing times or increases in anesthetic doses; however, serum biochemistry is altered by the use of

ketamine and so a two step process might not suffice should these values be collected in the future.

3. Although there were no significant differences between processing times and anesthetic doses used when a single or two animals were processed at one time, we found that team efficiency improved greatly when a single animal is processed, and recommend this method for the future.

4. This protocol is effective because of the high recapture rate and habituation to the traps by the animals.

5. New immigrants into groups do not affect trap habituation significantly but they do negatively impact the habituation to the observer.

Chapter IV: Dentition and Age-grades of *Saguinus fuscicollis* and *S. imperator*

IV. 1: Introduction

The series of changes undergone by an organism from birth to death is termed its life history, and is described by variables such as reproductive output, mortality and survivorship (Harvey & Clutton-Brock 1985). Life histories can be compiled for a population, and compared across different taxa and habitats, allowing us to describe species specific patterns that have evolved for success in a particular environment, as well as similarities in life history patterns across taxa (Godfrey et al. 2001; Harvey & Clutton-Brock 1985). Since the probabilities of survival and the production of offspring differ across animals of different ages, the age-structure of a population is critical to understanding the selective pressures on life history.

Population viability analyses (PVA) use life history data from long-term studies to create models that predict the sustainability of a population in the future (Beissinger & McCullough 2002; Crouse et al. 1987; Morris et al. 2002). A recent analysis of 21 long-term ecological studies used the first half of data collected to create a model, and verified the predicted outcomes with the second half of data, which reflected the true otucomes; they confirmed that the risk of population decline predicted by the model closely matched observed outcomes, making PVA a strong tool for conservation (Brook et al. 2000). Due to the complexities of following a cohort from birth to death, there is, however, remarkably little longitudinal data available on free-ranging populations of relatively slow-growing non-human primates with known ages. Moreover, even if age is assessed once, new individuals, whose ages remain unknown and can only be estimated, regularly disperse into a study population (Galbany et al. 2011). For the primate order, consisting of over 400 species, there have only been *ca*. 18 field studies of wild populations lasting longer than 10 years (Clutton-Brock 2012). The majority of research involves observing populations across a subset of years at regular intervals, resulting in cross-sectional or minimal longitudinal data. Although most populations exhibit stable age distributions, the precise age of any individual can rarely be determined with confidence. This

problem is particularly accentuated for adults. Once adult body size is achieved in a primate, there are virtually no visible, quantifiable, or consistent changes in morphology that reliably correlate with incremental increases in age. Conversely, infants display a variety of morphological and behavioral changes – in feeding behavior, independence, visible size, pelage colorations or relationships with adults – that can be readily associated with increasing age or age categories (e.g. infant, juvenile, or subadult) (Altmann & Altmann 1981; Garber & Leigh 1997; Ingram 1977; Treves 1997).

To overcome these difficulties, capture-and-release programs have been used to acquire data on dental conditions of wild primates at regular time intervals (Cuozzo et al. 2010; Dennis et al. 2004; Galbany et al. 2010; Kahumbu & Eley 1991; King et al. 2005; M'kirera & Ungar 2003; Nystrom et al. 2004; Phillips-Conroy et al. 2000; Yamashita 1998; Zihlman et al. 2004; Zohdy 2012). These data can reveal eruption states of teeth in young individuals, as well as occlusal wear on the permanent dentition of older animals. Although there are substantial differences between populations of the same species, and even between individuals, based on behavior, lifestyle and diet (as evidenced in the case of humans) (Mays 2002; cf Smith 2005), dental condition is still the closest marker for age for many species. Age-grading methodologies based on changes in dental condition are particularly important in species with complicated sexual development. This is well exemplified in the primate family Callitrichidae, where reproductive suppression has been shown to delay sexual maturation (Tardif 1984). In these cases, determining an individual's age-class based on teeth as opposed to genital morphology avoids the risk of underestimating the ages of individuals who are sexually suppressed.

IV. 1. 1: Brief Study Outline

In this chapter I assign each animal to an age class based on their dental molds, and I use these data to populate age-class transition tables. Specifically, for both *Saguinus fuscicollis* and *S. imperator* I use dental eruption sequences for individuals < 1 y of age, and wear on the

mandibular molars for individuals > 1 y to estimate age class. These data are then entered into transition tables, based on life history theory, to predict the movement of animals from one class to the next. Since the causes of disappearances of individuals from the monitored population remain unknown, I project a variety of scenarios with differing assumptions, such as death or dispersal, and test the flexibility of the generated model. Although the data here are preliminary, and their predictive outcomes will require testing in the future, I use stage-based population viability analyses in this case to assess the probabilities of survival of individuals of one age class till they transition into the next age class.

IV. 1. 2: Occlusal Wear and Age

Research indicates that age is reflected in occlusal tooth wear of wild nonhuman primates: lemurs (Cuozzo et al. 2010; King et al. 2005; King et al. 2012; Zohdy 2012), baboons (Galbany et al. 2011; Galbany et al. 2010; Nystrom et al. 2004; Phillips-Conroy et al. 2000; Swindler & Meekins 1991), howler monkeys (Dennis et al. 2004), macaques (Kay & Cant 1988; Schultz 1935), and the great apes (M'kirera & Ungar 2003; Schultz 1935). Tooth wear has also been related to individual fitness (Cuozzo & Sauther 2004), stress (Dirks et al. 2002), habitat quality (King et al. 2012), and most commonly, diet (Deane 2012; Rosenberger & Kinzey 2005; Teaford & Oyen 1989; Ungar 1990; Wright & Willis 2012; Yamashita 1998), particularly in human populations(cf Smith 2005). Therefore, in order to use occlusal wear as a marker for age, one must compare individuals within a population where at least diet remains relatively similar, and the rate of wear is not slow enough that secondary factors could cause interindividual differences (Mays 2002).

While tooth wear provides an estimation of age, the confidence level of the analyses can be affected by other factors. First, selecting a single tooth or multiple teeth to assess wear can be influential – selected teeth should generally be subject to minimal individual variation (for e.g., canines would be a bad choice) or early tooth loss, and must be easily visible on casts for

assessment. Moreover, the same teeth must be used for comparison because wear patterns differ with time since eruption and occlusion based on the location of the tooth in the jaw. Second, methodology for assessing wear patterns must be selected independently for each population, since interspecific differences in tooth morphology can affect the characters used to stage teeth. For example, while cementum annulus counts on first molars have been used to age the Cayo Santiago macaques fairly accurately (Kay & Cant 1988), these might not be visible on much smaller teeth of callitrichids, or might not even follow an annual cycle. Finally, in an ideal situation, one should sample a population representing all stages of tooth wear, with a schedule relating tooth wear to chronological age (Phillips-Conroy & Jolly 1988; Swindler & Meekins 1991).

IV. 1. 3: Dental Eruption Sequences

For younger individuals, in addition to observable differences in size, behavior and morphology, dental eruption sequences can be of enormous use in assigning ages. The most comprehensive records we have of dental eruption sequences come from work on skeletal remains from museums or animals in captivity (Byrd 1981; Chase & Cooper 1969; Glassman 1983; Harvati 2000; Henderson 2007; Holly Smith et al. 1994; Schultz 1935). However, a few long-term studies of wild populations of primates have provided a comparative viewpoint to determining exact timing of dental eruption in the wild (Conroy & Mahoney 1991; Phillips-Conroy & Jolly 1988). These comparisons show that the schedules of development in captive animals underestimate age in wild animals, which take longer to mature (Kahumbu & Eley 1991; Phillips-Conroy & Jolly 1988; Zihlman et al. 2004), and some teeth show greater inter-individual variability in age at eruption than others. This suggests that aging young individuals by the presence or absence of a single tooth is not reliable in wild populations (Kahumbu & Eley 1991). It is advisable, therefore, to consider the entire dental complement in young individuals. Further, sex differences in age at eruption of individual teeth must not be ignored (Phillips-Conroy & Jolly 1988).

IV. 1. 4: Dentition and Age in the genus *Saguinus*

Previous research on dental variation among tamarins includes work by Chase and Cooper (1969) on *S. nigricollis* eruption sequences and timings, Hershkovitz (1977b) on eruption sequences (but not timings) in 5 *Saguinus* spp., Natori (1988) on nonmetric features of 10 *Saguinus* spp., Swindler on metrics of *S. geoffroyi* teeth (2002), and Tornow et al. (2006) on the metric features of wild *S. mystax*. The most recent of these studies on dental casts obtained from *Saguinus mystax* on Padre Isla in Peru, indicates that the second molars in this species are more variable than the first molars in length, width and crown area (Tornow et al. 2006). Since tamarins lack a third molar (Hershkovitz 1970), which is typically hypervariable among primates (Gingerich & Schoeninger 1979), their second molars take on the function of third molars in other primates. Comparisons to other species of tamarin indicate that *S. mystax* is not unique in this regard, and imply that M1 is the least variable of the cheek teeth in *Saguinus* (Tornow et al. 2006).

Dental eruption sequences have been determined through different datasets of skeletal materials for *Saguinus fuscicollis* and a few other tamarin species (but not *S. imperator*) (Byrd 1981; Chase & Cooper 1969; Glassman 1983; Henderson 2007; Schultz 1935; Soini & Cóppula 1981). Eruption of the deciduous teeth of *S. fuscicollis* is known from studies of 62 skulls by Glassman (1983) and 7 captive individuals by Soini (1981). They show that these animals are born with deciduous incisors and canines in both jaws, as well as the first deciduous premolar in the mandible. Between 2 and 12 weeks of age, the remaining deciduous premolars erupt in both jaws (Table IV. 1A) (Glassman 1983).

Table IV. 1A: Dental eruption sequences for deciduous teeth adapted from Glassman (1983)

Maxilla	**I1**	**I2**	**C**		**M1**	**M2**		**M3**
Time (wks)	Birth	Birth	Birth		2	2-5		6-12
Mandible	**I1**	**I2**	**C**	**M1**		**M2**	**M3**	
Time (wks)	Birth	Birth	Birth	Birth-2		2-5	5-8	

The eruption of permanent dentition in the genus *Saguinus* has been examined in some detail, with slightly different modal eruption sequences presented for a few populations (common in humans cf Smith & Garn 1987). All studies (Byrd 1981; Glassman 1983; Henderson 2007; Soini & Cóppula 1981) agree that the first molar and both incisors erupt first in sequence (M1, I1, then I2), and that there are no sex differences for eruption sequences in these species (Table IV. 1B). Some studies indicated differing schedules of eruption for the remaining teeth either jaw, with no agreement on whether mandibular or maxillary teeth erupt first (Byrd 1981; Glassman 1983; Soini 2001). Glassman's examination revealed some variation in whether m2 erupted before p4 in the maxilla, but was certain that M2 erupted first in the mandible (1983). Byrd (1981) and Soini (1981) agreed with Glassman in that m2 and M2 erupt first, but then indicated that there is much variability in the subsequent eruption sequences of the premolars (Table IV. 1B). Henderson's (2007) 15 specimens of *Saguinus* spp. contributed no information to the eruption sequences of the premolars, but confirmed that the canines were the last permanent teeth to erupt in both jaws, as seen in other studies (Byrd 1981; Glassman 1983; Soini & Cóppula 1981). Glassman (1983) and Soini (1981) also attributed approximate ages to the eruption sequences, neither very different from the other. Due to the larger sample size, I use Glassman's calibration to determine the ages of animals in this study that are < 1 y old (Table IV. 1C).

Table IV. 1B: Dental eruption sequences for permanent teeth of various *Saguinus spp*. derived from three available studies.

Reference Source	Dental eruption sequence for permanent dentition
Glassman (1983)	M1 • I1 •I2 • (M2 •P4) • P2 • P3 • C
(*S. fuscicollis*)	M1 • I1 • I2 • M2 • P4 • P2 • P3 • C
Henderson (2007)*	M1 • I1 □ I2 • M2 • P4 • P2? • P3? • C
Saguinus spp.	M1 • I1 • [I2 •M2]• P2?• P3?• P4? •C
Byrd(1981)	M1• I1 • I2 • M2 • P4 • (P3 • P2) • C
(*S. fuscicollis*)	M1 • I1 • I2 • M2 • (P4 P2) • P3 • C
Soini (1981)	
(*S. fuscicollis*)	M1 •□I1 • I2 • M2 • P3 • P2 • P1 • C
	M1 • I1 • I2 • M2 • P3 • P1 • P2 • C

* no premolars were available in this dataset for *Saguinus* spp. No sex differences specified.

Table IV. 1C: Dental eruption timings for permanent teeth for *Saguinus fuscicollis*

Maxilla	**M1**	**I1**	**I2**	**M2**	**P4**	**P2**	**P3**	**C**
Time (mo)*	3.9	4.6	5.5	6.8	6.7	7.4	7.2	8.7
Time (mo)**	4.5-5.8	5.3-5.8	5.3-7.3	7.3-9.8	7.3-9.8	8-9.8	9.5-9.8	9.8-11.3
Mandible	**M1**	**I1**	**I2**	**M2**	**P4**	**P2**	**P3**	**C**
Time (mo)*	3.7	4.6	5.2	6.2	6.9	7.2	7.5	9.0
Time (mo)**	4.0-5.8	5.3-5.8	5.8-7.3	7.3-7.8	7.3-9.8	8.0-9.8	9.3-9.8	9.8-11.3

* adapted from Soini (1981)

** adapted from Glassman, converted from weeks to months (1983)** Table IV. 1D**. Canine sizes based on age, relevant during transition from juvenile to subadult age categories. Note, cannot be used on deciduous canines or worn canines on adults. Adapted from Soini (1981)

IV. 1. 5: Ageing the Study Population

Eruption sequences based on captive animals underestimate age of wild animals to at least some extent (Kahumbu & Eley 1991; Zihlman et al. 2004), I am compelled to use the single study on *S. fuscicollis* that actually provides a calibrated time scale for eruption by Glassman (1983) as a reference. I will use two individuals of known ages to verify if these delays occur in my study population compared to Glassman's (1983) schedule. I also choose to primarily focus on the mandibular first molars for an analysis of occlusal wear, as they have been found to be the least variable cheek tooth in *Saguinus* spp. (Tornow et al. 2006). Although the primary reference for determining tooth eruption stage and age for both species is Glassman's (1983) study on *S. fuscicollis*, other studies on eruption sequences have shown that *Saguinus* spp. do not vary much in this regard; thus, *S. imperator* is likely to follow the same eruption sequence, and for the purposes of this study, I assume that it does (Byrd 1981; Henderson 2007). Therefore, both species will be age-graded using the same classes, but it is important to note that tying the age sequence to a precise time chronology need not necessarily be similar for both species.

Since this study cannot produce sufficient longitudinal data at the present time, chronological age cannot be correlated with occlusal tooth wear for these species. As such, traditional life tables charting life history are not feasible in this case. However, this is a common obstacle since longitudinal datasets are rare with long-living species such as primates (Clutton-Brock 2012), and other methods have arisen to assess life histories. Stage-based transitional life-tables, that utilize stage-specific vital rates (or age-class specific rates of survival and reproduction) instead of age-specific fertilities and mortalities (Alberts & Altmann 2003), can be used to estimate the probabilities of animals moving from one age-class or stage to another. In this transitional stage-based model, vital rates are age-class specific, instead of age-based.

Using this transitional model, I test if males and females of each species exhibit similar vital rates, which is possible given a lack of sexual dimorphism in this species and male and female dispersal. I also test if the two species vary in their vital rates and stable stage distributions based on age-class. To do so, I use a birth-pulse model, since both species are known to reproduce seasonally (i.e. the wet season). I use post-breeding censuses to populate this model, since data were collected once each year per animal from April to July, within 6 months of the breeding season.

IV. 2: Methods and Analyses

IV. 2. 1: Dental casting

Dental casts were obtained from sedated individuals at least once a year, and for a few *S. fuscicollis*, multiple times in a year. I used a vinyl polysiloxane impression material (ESPE Imprint Garant II, Defend®, Regular set, Light Body) to obtain molds of both jaws for each animal. First, I deposited the material along the dental arch of the mandible of each animal, quickly inserted a slim but firm piece of plastic over the mandibular teeth, and then deposited more impression material onto the plastic. At this stage, the upper jaw was allowed to close and the mouth pressed shut with light pressure for *ca.* 1.5 min until the material had set. The small plastic sheet allows for separate impressions of both jaws without canines from one jaw puncturing the other. Each mold therefore captured a good impression of at least one half of the mandibular and maxillary dentition for each animal.

Every mold was first carefully trimmed until only the dental arch for each jaw was remaining. Both sides of the mold were sprayed with a thin mist of universal mold release (Smooth-On®). Then, plasticine cups were created for each mold, and carefully manipulated to fit each mold. I mixed the two solutions of a low viscosity, super light, liquid plastic casting material (Alumilite®) in equal volumes, and added a slight brown tint (Polytek® polymer) to the mixture, which was then poured into each clay cup. The cups were centrifuged to force bubbles

away from the apices of the teeth, and allowed to set for at least 2 min. Each cast was carefully extracted from the molding material and analyzed under a 30X stereoscopic microscope.

IV. 2. 2: Assigning Age-Classes

For each animal for which a dental impression had been obtained during the study, I examined the dental cast in association with canine lengths (measured from the tip of the canine to the gum line on both upper quadrants and then averaged), as well as the images of teeth taken during the capture process. First, I identified all deciduous teeth, erupting teeth not in full occlusion, and fully erupted permanent dentition for each animal from the casts. If animals had any deciduous teeth, then I could use Glassman's (1983) age-calibration to identify an approximate age for them (Tables IV. 1D and IV. 2A).

Table IV. 1D: Dental eruption timings for canines of *Saguinus fuscicollis*

Canine length (mm)	2.0	2.5	3.0	3.5	4.0#	4.5#	5.0#
Months	9	9½	9½	10	11	11½	13

possible variation of up to a month for these categories

Table IV. 2A: Infant age-categories based on (+) Glassman (1983) and (∞) Soini (1981).

Category	**Known age+∞**	**Features**
Ia	0-1½ mo	dI1, dI2, dC, dM1, dM2 present on both jaws
Ib	1½-3 mo	dM3 erupts first on the mandible then the maxilla
Ic	4½-5¾ mo	M1 erupts, and I1 from 5¼-5¾ mo
Id	5¾-7¼ mo	I2 erupts
Ie	7¼-9¾ mo	M2 erupts and then P4, P2, and P3 erupt, most likely in that order but not always
If	9¾-11¼ mo	Canines erupt, ranging from 2 mm at 9 mo to 4 mm at 11 mo
Ig	11½-13 mo	Canine length goes from 4.5 mm to 5 mm but could vary by up to 1 month

d = deciduous; p = premolar; M = permanent molar; number after the designation indicates position in the tooth row and jaw type i.e. M^2 is the second permanent molar on the maxilla

If a first molar had erupted, I then examined all available first molars on four quadrants for occlusal wear. Each cusp in the tooth was categorized as one of the following: unworn, worn (wear facets visible), dentin lakes (visible patches of dentin present on each cusp), dentin crescents (dentin lakes so big that they fuse together buccal-lingually), and flat (worn down completely flat). Based on these characterizations, I identified four major age-classes (ACs), each with a few internal wear categories (WCs) determined by combinations of wear-levels for all four cusps of each mandibular molar (Table IV. 2A, Fig. IV. 1). WC 1, 2, and 3 were observed in animals who still had to acquire their complete permanent dentition, and therefore, ages can be identified for animals up to an early WC 3. WCs 4 and 5 as well as older WC-3 individuals are definitely older than 1 y and display the full range of variation in molar tooth wear for these species.

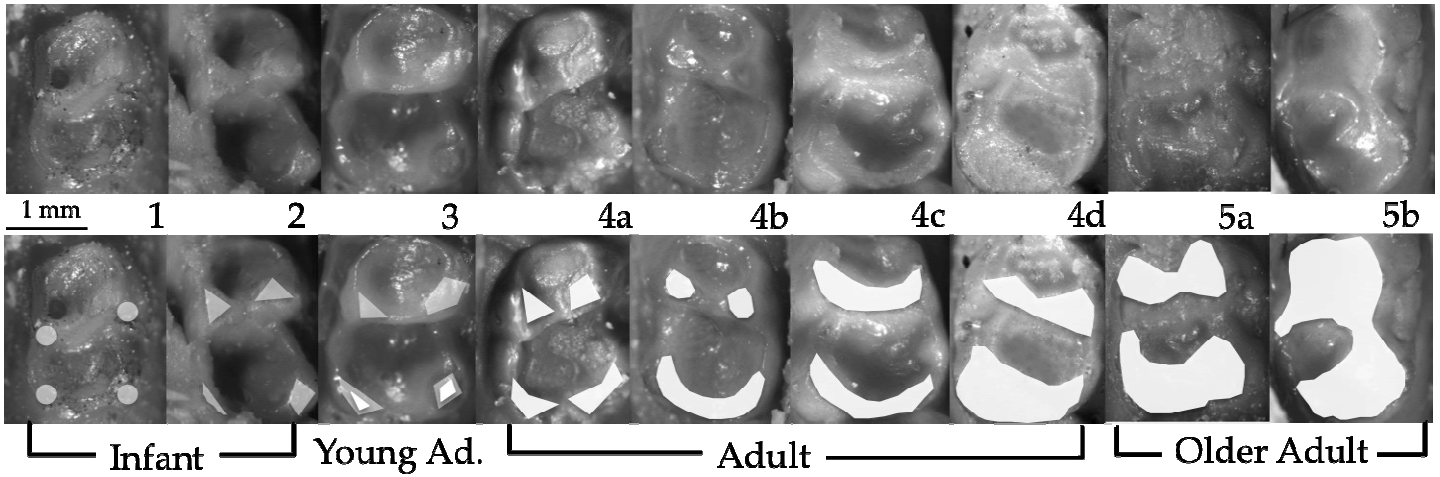


Figure IV. 1. Mandibular molars categorized into wear categories 1-5b, which are then classified into four age-categories (infant, young adult, adult and older adult). The lower frames are identical to the upper frames, but have dental wear highlighted. Light grey highlights indicate wear facets, and the white highlights are dentin showing through the enamel of the teeth.

In cases where multiple mandibular first molars were available, I used the WC from the most complete tooth, i.e., the one with all four cusps visible. If two such teeth were available and the WC was not the same for both (for example, due to malocclusion or biased usage of one side of the mouth by the animal), then, since all teeth had at least as much wear as the least worn tooth, I used the tooth with the lower WC to classify the cast as a whole. In order to avoid bias, I did not refer to the identity of the individual or its photographs until after the cast had been scored. After scoring, I also examined the casts within each WC to make sure that they were internally consistent with the scoring scheme. Finally, I scored all casts three times in this manner and used the most commonly assigned WC as the final score. The final four ACs obtained were AC infant (including WCs 1 and 2), AC 1, or young adult (WC 3), AC 2, or adult (WC 4a – 4d) and AC 3, or old adult (WC 5a and 5b) (Table IV. 2B, Fig. IV. 1). The distributions of individuals assigned to each of the four classes were positively correlated between species (r = 0.999), and between the sexes for each species (*S. fuscicollis:* r = 0.986; *S. imperator*: r = 0.933)

Table IV. 2B: All age-categories for *Saguinus fuscicollis* and *S. imperator*. These are based on (+) Glassman (1983) and (∞) Soini (1981), as well as occlusal wear patterns for the mandibular first molars. Known ages are not available for any categories, except possibly categories 2 and 3.

Category	Age-Class	Features on Mandibular M1
1	Infant	No wear
2		Wear facets visible but no dentin
3	Young Adult (1)	Dentin on hypoconid and entoconid, but just wear on protoconid and metaconid
4a	Adult (2)	Dentin lakes on one or more cusps, but no continuous crescents
4b		Dentin crescents continuous on hypoconid and entoconid, but just dentin lakes on protoconid and metaconid

Table IV. 2B. ***Continued***

4c		Two dentin crescents, one each in the talonid and trigonid basins
4d		Dentin crescent in the trigonid but flat tooth in the talonid basin
5a	Old Adult	Flat cusps in both basins, but basins still discernible
5b	(3)	Completely flat tooth

IV. 2. 3: Age Structure

I assessed the age structure of the two species by pooling all available aged individuals per AC and including only one classification per individual each year for those that were assessed more than once a year. Chi-square tests were used to test for differences between age-structures of the two species, as well as between sexes within each species ($\alpha = 0.05$).

IV. 2. 4: Stage-based Transition Tables

Transition tables are useful for the analysis of the life history of individuals in a population when exact ages are not available (Fig. IV. 2A) (Crouse et al. 1987). They use census data pooled across different years for those individuals for which at least two censuses are available. Transition tables begin with the numbers of animals across age-classes observed in the population, as well as the fates of each animal at the second census point (transition or not to the next age-class, death, or dispersal), to predict the probabilities of an individual moving from age-class a to b, listed as $P_{a,b}$ (Fig. IV. 2B). Then, specific fecundities ($F_{a,b}$), defined as the number of infants (of either sex) born to females in an age class, were calculated for those age-classes that were reproductively active. These probabilities and fecundities are arranged in a projection matrix suggested by Lefkovitch (1965), based on modifications of Leslie (Leslie 1945)matrices (see Crouse et al. (1987) for a detailed review). Since this is a stage-based model, the probabilities within the matrix are termed vital rates, which are age-class specific, but not age-dependent.

By multiplying this matrix by a vector containing the observed numbers of individuals in each age class, the cross-products will predict a second vector of the numbers of individuals at time t+1. This probability matrix then can extrapolate the numbers of individuals at subsequent

times, separated by the assigned interval of time, known as the projection interval. The population growth rate (λ) between any two time points is the ratio of the total number of individuals in time t+1 to time t. These figures are then projected until a stable value of λ is obtained, referred to then as the asymptotic growth rate of the population.

The life cycle model used in this analysis assumes four distinct stages: infant, young adult or subadult, adult and old adult (Fig. IV. 2A). Since I have two yearly censuses for *Saguinus imperator*, as compared to three for *S. fuscicollis*, the model for *S. fuscicollis* is necessarily more robust. I included all individuals with known age-classes and fates between any two censuses, and the data were pooled for all available years, so some of the same animals may be reassessed if present in subsequent years. Within the censused population as a whole, several individuals were missing during the second census point. The following guidelines were used to assign fates to these individuals. If an animal in the infant age-class or the old-adult age-class was missing at a second census point, since these individuals were probably too young or too old to disperse, I assumed that they were dead. In both species, both sexes were found to disperse (as part of a different analysis) and all known individuals that dispersed were of the adult age-class. Therefore, for those individuals in this class who were never located and assessed in a subsequent year, I could not be sure if death or dispersal were the reason for their disappearance. Different approaches were utilized to create projection matrices to account for the possible fates of these missing individuals as follows:

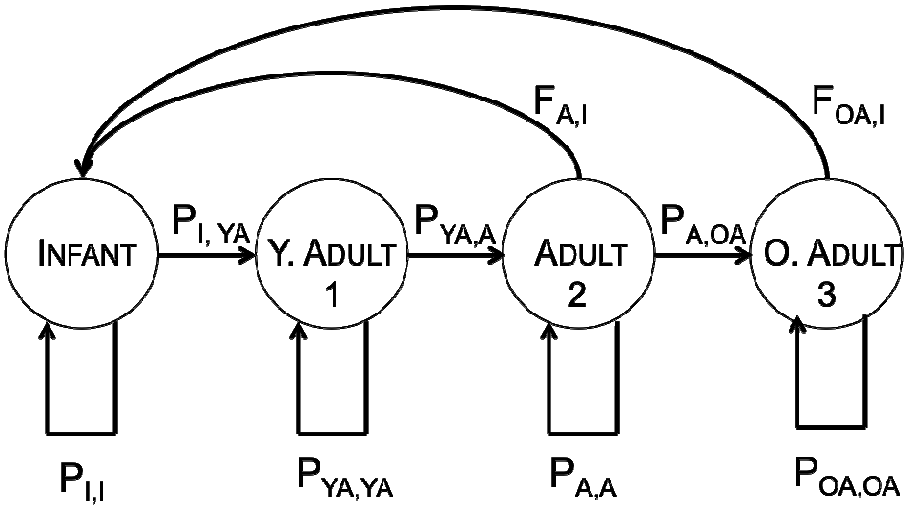


Figure IV. 2A: A life cycle model for both callitrichid species based on distinct age-classes identified after occlusal tooth-wear analyses. The circles indicate each age-class or stage. The arrows connecting the circles indicate the probability of an individual transitioning from one class to the next. The square arrows below indicate the probability of an individual remaining in the same class. The curved arrows above represent the fecundity of a particular age-class and are illustrated only for adult and old adult classes, since these are the only reproductively active age-classes for these species.

$$M = \begin{bmatrix} P_{INF,\ INF} & F(YA)=0 & F(A) & F(OA) \\ P_{INF,\ YA} & P_{YA,\ YA} & P_{A,\ YA} & P_{OA,\ YA} \\ P_{INF,\ A} & P_{YA,\ A} & P_{A,\ A} & P_{OA,\ A} \\ P_{INF,\ OA} & P_{YA,\ OA} & P_{A,\ OA} & P_{OA,\ OA} \end{bmatrix}$$

Figure IV. 2B: A 4 x 4 Lefkovitch matrix of probabilities of transitioning from one age class to another (Lefkovitch 1965). Many of these probabilities will necessarily be zero, because the classes are organized in order of increasing age so animals will not transition backwards through these stages.

Case A: These individuals were excluded from the analysis entirely, because their fates remain unknown.

Case B: All such individuals were considered dead.

Case C: all such individuals were considered to have successfully dispersed, but alive and present in the same age-class.

Transitional models require a projection interval, or the length of time over which vital rates are measured. I chose a projection interval of 1 year, regardless of the durations of each age-class in the study, because this is the average amount of time between each consecutive census of the study population. In defining age-classes, I ensured that first, each class must be distinct from the next based on tooth wear, and thus, reflecting chronological age, and second, classes must not include too many individuals with varying vital rates, to avoid inflation of the survival of any one class (Alberts & Altmann 2003). To fulfill the latter condition, I could split the early age-classes into multiple groups, but due to the fast life histories of callitrichids, this would make early age-classes last only a few months each, many of which will be entirely missed by the yearly census conducted. Therefore, all infants were ultimately placed in a single age-class even though more fine-grained age-classes are available and will be used for other analyses.

Finally, I make a few simplifying assumptions to evaluate this model. I assume that a) all newborns were counted in each census, b) that censuses were taken within 6 months of the births occurring, c) all females give birth at approximately the same time each year and close to their own birth dates (supported in Chapter VI), and e) that the dominant female in each group is most likely to be the breeding female in the group.

IV. 3: Results

IV. 3. 1: Age-structure

The proportions of individuals in each age-class were found not to be significantly different between the two species, $\chi^2 = 5.1$ (df=3, N=137, $p>0.05$) (Fig. IV. 3). When individual sexes were examined by age-class in each species, no significant difference between the sexes was detected for either species: *S. fuscicollis*, $\chi^2 = 1.7$ (df = 3, N=88, $p>0.05$) and *S. imperator,* $\chi^2 = 1.6$ (df=3, N=49, $p>0.05$) (Fig. IV. 4). Overall age-structure for both species implies that age-class 2 or the "adult" class could likely represent many years in the life span of these primates, but that individual variation is high and so WCs 4a-4d that make up this age-class could not be reliably arranged in a precise chronology consistent across individuals.

Further, since each individual in the adult age-class must necessarily have passed through the young adult age-class, the ratio of the number of individuals in each class could be used to create a scaling coefficient. This coefficient, when multiplied by the duration of the young adult AC, can provide an estimate of the duration in months of the adult AC. Using the ages of the oldest individuals of known age in the infant and young adult ACs, the maximum approximate durations of the young-adult AC was calculated for each species (*S. fuscicollis*: 10¼ mo, and *S. imperator*: 12 mo). Based on these calculations, the adult AC was found to last for longer in *Saguinus fuscicollis* than in *Saguinus imperator* (Table IV. 3.). Further, no *S. fuscicollis* old adult was observed to be alive in a subsequent year; however, *S. imperator* older adults were observed to remain in the older adult phase for at least two years, although further longitudinal data will be required to provide a maximum number of years that adults remain in this class before death.

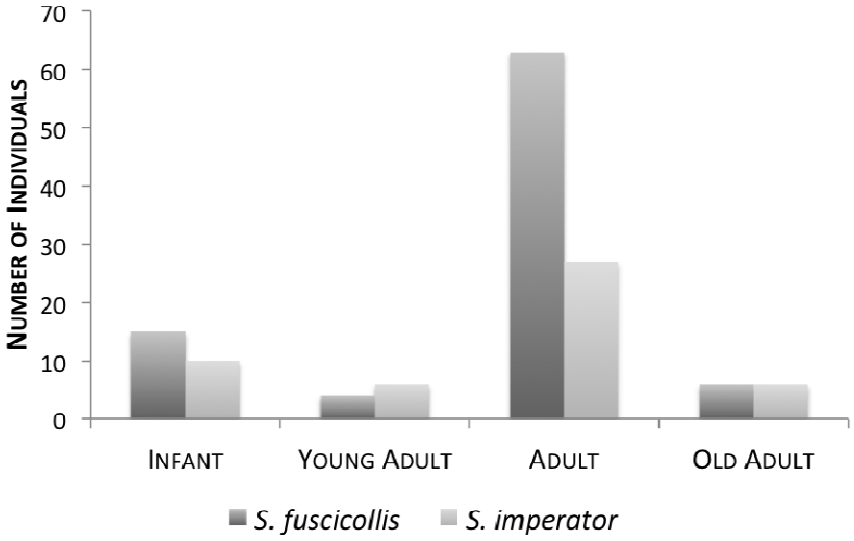


Figure IV. 3: Bar graphs of the age-class structure of *Saguinus fuscicollis* and *S. imperator*. No significant difference was found between the species.

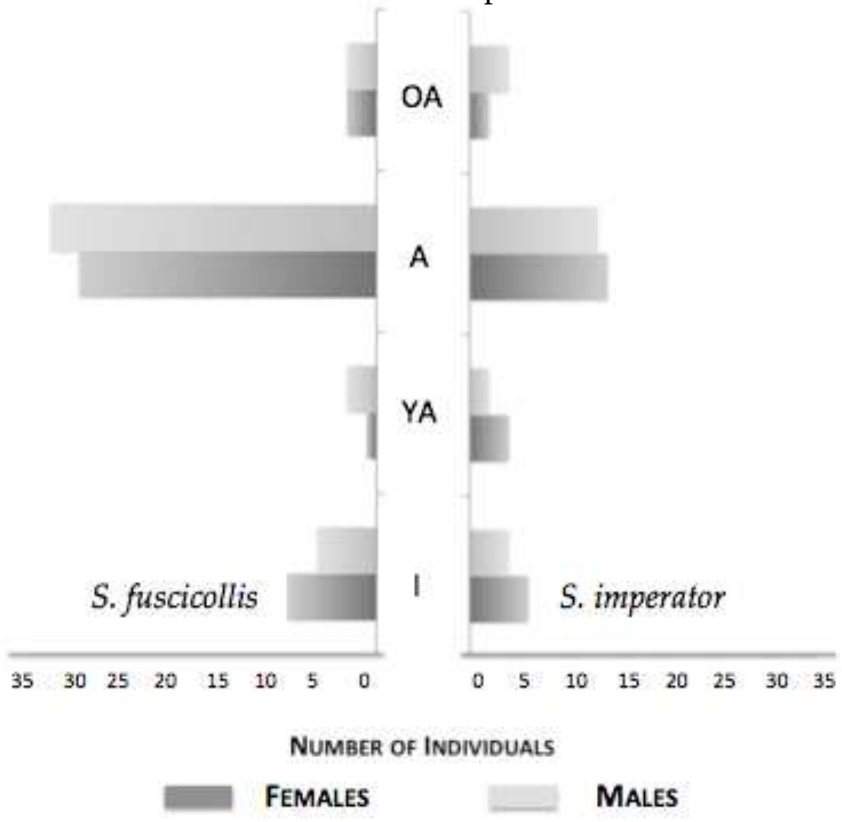


Figure IV. 4: Bar graphs of the age-class structure of *Saguinus fuscicollis* and *S. imperator* per sex. No significant difference was found between the sexes in each species.
I = Infant; YA = Young Adult; A = Adult; OA = Old Adult

The overall estimated durations of each AC are presented for each species based on these calculations (Table IV. 3). A key assumption for these predictions to hold true is that both species wear their teeth at the same rate. It is possible that *S. imperator* wear down their teeth slower than *S. fuscicollis*, in which case they could be older at all the transition events.

Table IV. 3: Estimated age-class durations estimated for each callitrichid species.

Species	**Age-Classes**			
	Infant	**1:YA**	**2:A**	**3:OA**
Saguinus fuscicollis	0-9¾ mo	9¾-20 mo (0.8-1.7 yr)	20-161□ mo (1.7-13.5 yr)	161□-173□ mo (13.5-14.5 yr)
Saguinus imperator	0-7¼ mo	7¼-19¼ mo (0.6-1.6 yr)	19¼-54 mo (1.6-4.5 yr)	54-78 mo (4.5-7.5 yr)

YA = Class 1, young adult; A: Class 2, adult; OA: Class 3, old adult

The brackets for the infant and young-adult ACs were determined based on the oldest individual within each AC and provide maximum estimates for these durations. The duration of the old adult AC is based on the longest interval for which an animal has survived within this AC for each species.

IV. 3. 2: Transitional Life Tables

Projection matrices for stage-based models of transition tables were constructed for a variety of scenarios (Fig. IV. 5). The vital rates of each age-class were calculated for cases where the fates of adults were unknown, using three assumptions as described in the methods section (Table IV. 4.). I found differing probabilities of transitioning or remaining in particular age-classes between the two species. In the case of *Saguinus fuscicollis*, the basic model (including only individuals with known fates) showed that all individuals moved from the young adult to adult AC without fail within a year ($P_{YA, A} = 1.0$), while invariably some young and old adults did not remain within their ACs and disappeared (Table IV. 4). We believe that while this is likely to be a legitimate reflection of age and increased mortality in the old adult AC, the young adult AC is inadequately sampled in this species as it extends for a shorter duration than the projection interval of 1 year (Fig. IV. 6). Of the other vital rates, $P_{A, A} > P_{INF, YA} >>> P_{A, OA}$ but $\neq 1.0$ implying that the adult AC represents many years in the lifespan of an individual, and that infants are joining this AC faster than adults are either dying or transitioning into the older adult AC. When

individuals with unknown fates in the second year in the adult class are assumed to be dead (Case B), all vital rates remain the same save for the $P_{A, A}$, which drops. The opposite trend is observed, when individuals with unknown fates, in the second year in the adult class, are presumed to have dispersed (Case C) (Table IV. 4). In general, the fecundity of the adult AC was slightly higher than the fecundity of the older adult AC in this population.

Saguinus imperator, unusually displayed a $P_{OA, OA} = 1$, because no individuals in the older adult AC were observed to disappear or die in this population up to this time. A quarter of the individuals (N = 4) in the infant AC transitioned into the young adult AC, while the same percent transitioned directly into the adult AC (Table IV. 4, Fig. IV. 7). Interestingly, infant mortality is 50% in this population, while only 33% in the *Saguinus fuscicollis* population (N = 9). In the basic model (Case A), 80% of young adult *S. imperator* (N = 5) transition into the adult AC, while only 15% (N = 7) transition into the older adult AC (Table IV. 4). Finally, young adults reproduce at a higher rate (67%) (N = 3) than adults (46%) (N = 13). In Case B, the $F_{(A)'}$, $P_{A, A}$, and $P_{A, OA}$ are halved from values in Case A, due to the high number of individuals in the adult AC with unknown fates. In Case C, however, $P_{A, A}$ returns to slightly higher than values in Case A, while other vital rates remain the same as in Case B. Overall, *Saguinus fuscicollis* exhibits a stable population growth rate that is higher than that of *S. imperator*; however, both populations are growing (Table IV. 4).

$$M_{SF} = \begin{bmatrix} 0 & 0 & 0.642 & 0.500 \\ 0 & 0 & 0 & 0 \\ 0.667 & 1.00 & 0.806 & 0 \\ 0 & 0 & 0.032 & 0 \end{bmatrix} \qquad M_{SI} = \begin{bmatrix} 0 & 0.667 & 0.667 & 0 \\ 0.250 & 0 & 0 & 0 \\ 0.250 & 0.800 & 0.857 & 0 \\ 0 & 0 & 0.143 & 1.00 \end{bmatrix}$$

$$M = \begin{bmatrix} P_{INF,\,INF} & F(YA)=0 & F(A) & F(OA) \\ P_{INF,\,YA} & P_{YA,\,YA} & P_{A,\,YA} & P_{OA,\,YA} \\ P_{INF,\,A} & P_{YA,\,A} & P_{A,\,A} & P_{OA,\,A} \\ P_{INF,\,OA} & P_{YA,\,OA} & P_{A,\,OA} & P_{OA,\,OA} \end{bmatrix} \qquad M_{SF\text{-}F} = \begin{bmatrix} 0 & 0 & 0.643 & 2 \\ 0 & 0 & 0 & 0 \\ 0.800 & 1 & 0.643 & 0 \\ 0 & 0 & 0.071 & 0 \end{bmatrix}$$

Figure IV. 5: Lefkovitch matrices for the following populations: for *Saguinus fuscicollis* Case A (MSF), *S. imperator* Case A (MSI), female *S. fuscicollis* only (MSF-F) based on four age-classes. Reference matrix present at bottom left.

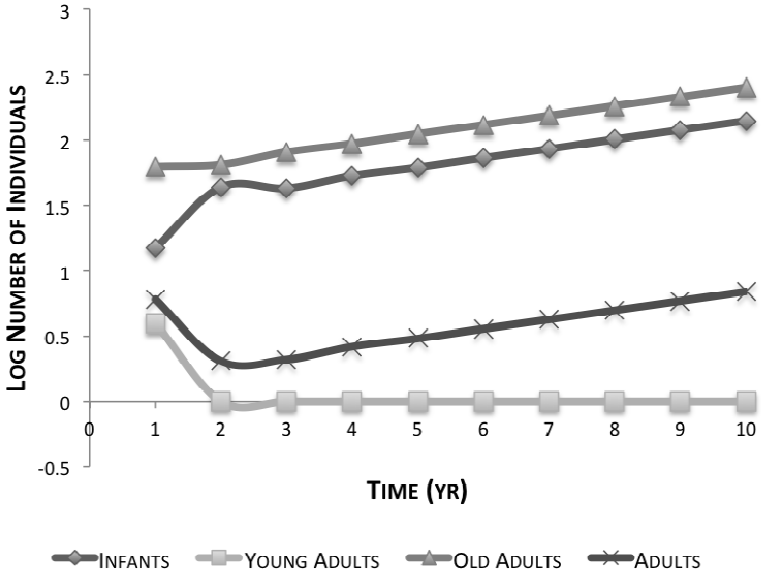


Figure IV. 6: Graph of the number of individuals predicted by the model in each age-class over time for *Saguinus fuscicollis*. The model is based on the Lefkovitch matrix for this species in Figure IV. 5.

Table IV. 4: Transitional life tables and vital rates for four age-classes per species.

Species	Vital Rates							Fecundities				
	$P_{INF, YA}$	$P_{INF, A}$	$P_{YA, YA}$	$P_{YA, A}$	$P_{A, A}$	$P_{A, OA}$	$P_{OA, OA}$	F (YA)	F (A)	F (OA)	λ	N
S. fuscicollis Case A	0	0.667	0	1.00	0.806	0.032	0	0	0.642	0.500	1.178	45
S. fuscicollis Case B	0	0.667	0	1.00	0.758	0.030	0	0	0.600	0.500	1.178	47
S. fuscicollis Case C	0	0.667	0	1.00	0.818	0.030	0	0	0.600	0.500	1.178	47
S. imperator Case A	0.25	0.25	0	0.800	0.857	0.143	1.00	0.667	0.667	0.00	1.142	18
S. imperator Case B	0.25	0.25	0	0.800	0.462	0.077	1.00	0.667	0.400	0.00	1.142	24
S. imperator Case C	0.25	0.25	0	0.800	0.923	0.077	1.00	0.667	0.400	0.00	1.142	24
Female *S. fuscicollis*	0	0.800	0	1.00	0.643	0.071	0	0	0.643	2.00	1.167	21

The asymptotic growth rate linked to each model is also reported

Case A: All adults without known fates excluded

Case B: All adults without known fates assumed dead

Case C: All adults without known fates assumed alive and dispersed

PA,B = probabilities of transitioning from Class A to Class B

F(A) = Fecundity of animals in Class A

YA = Class 1, young adult; A: Class 2, adult; OA: Class 3, old adult

λ = the asymptotic growth rate at year for the proposed model

N = the number of animals for which data on dentition exist at two time points

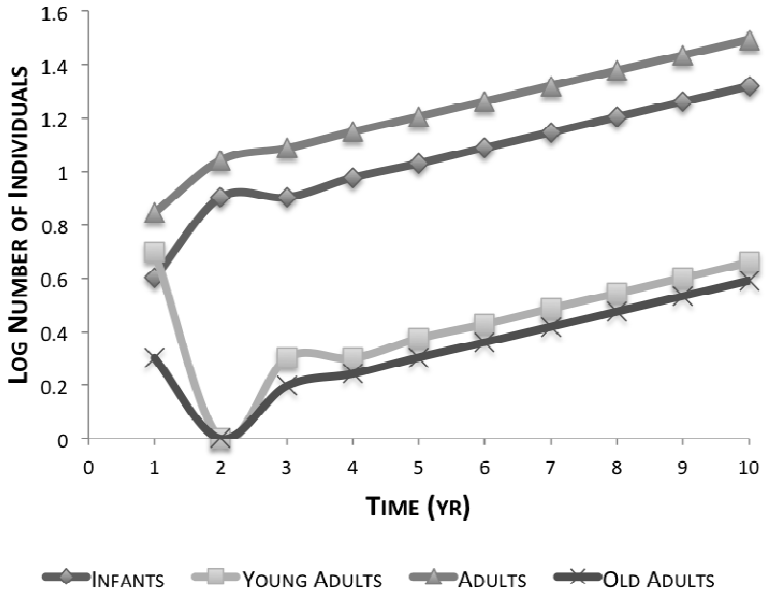


Figure IV. 7: Graph of the number of individuals predicted by the model in each age-class over time for *Saguinus imperator*. The model is based on the Lefkovitch matrix for this species in Figure IV. 5.

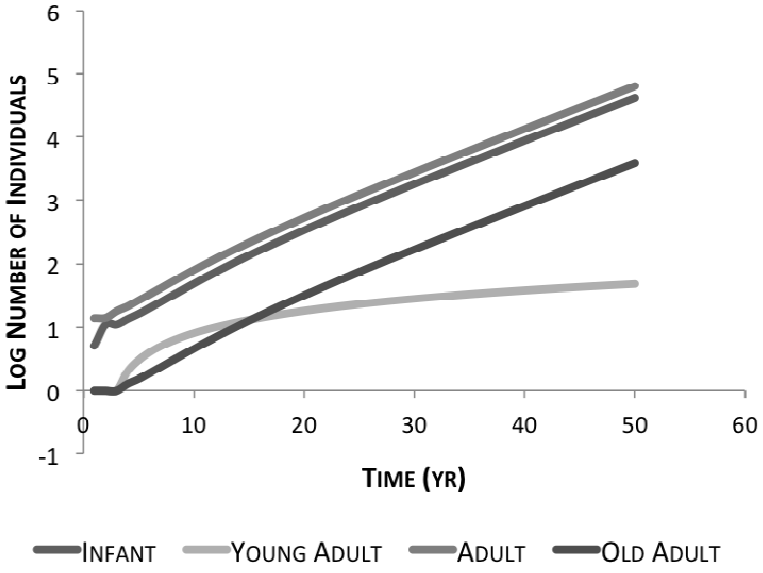


Figure IV. 8: Graph of the number of females predicted by the model in each age-class over time for *Saguinus fuscicollis*. The model is based on the Lefkovitch matrix (1965)for females of this species as presented here. There are too few females present in the *S. imperator* population to conduct the same analyses.

Finally, it was possible to assess a female-based model for *Saguinus fuscicollis*, since adequate numbers of females were available after three years of sampling (Figure IV. 8). Interestingly, when only females are included, the fecundity of the older adult AC rose to two offspring per female, while that of the adult AC, remained the same as the Case A model (Table IV. 4). Infant mortality dropped to 20%, and while 65% of adults (N = 14) remained within the adult AC, 7% moved to the older adult AC, which is double the rate of the basic Case A model. Figure 8 shows a lower asymptote for the young adult females, implying a higher attrition rate in that age class even under a stable age-class distribution.

IV. 3. 3: Verification of Dental Eruption Sequences and Timings

During this study, we were fortunate to be present at the birth of twins of *Saguinus fuscicollis* in 2009, and therefore, the exact day of their birth is known. This allows us to verify if the age-class in which they were placed based on Glassman's (1983) eruption schedule is coordinated with their chronological age. I found that their ages were routinely over estimated based on the published schedule for captive-raised animals, with the actual age falling at or just below the lower end of the age-bracket provided by Glassman (1983) (Appendix IV. 1A).

I also observed that all individuals graded as WC 2 (Table IV. 2B) based on the wear of their mandibular first molars, could be calibrated to an age-class of 5¾ to 9¾ mo in both species. The majority of animals in this category of tooth wear were estimated to range from 5¾ to 7¼ mo of age for *S. fuscicollis* (38.5% of 26 animals), whereas in *S. imperator*, the majority was aged 7¼ to 9¾ mo (67% of 9 animals). Further, all individuals of Category 3 (Table IV. 2B) in *S. fuscicollis* were calibrated to 9¾ to 11¼ mo (N = 3) whereas this could not be said of any of the Category 3 *S. imperator*. This implies a differential schedule of tooth wear tied to age for the two species, specifically *S. imperator*. As many as 85% of the individuals remained within the adult AC, implying that this class has an extended duration in this species.

IV. 4: Discussion and Conclusions

Long-term studies of slow-growing primates have the distinct advantage of identifying life history characteristics of the individuals in the population that can be tied to their known ages. Individuals born to the first cohort in the study are typically best known, while individuals that immigrate into the population are the least understood in this context. In this study, with a maximum of three years of longitudinal data available, other measures are necessary to understand life history dynamics over the lifespan of an individual. However the basic outcomes suggested by these data can be verified by future years of work to confirm the validity of using population viability analyses for these species (Brook et al. 2000).

First, an aging schedule was developed to accurately determine an age-class for each individual in the population. For individuals born during the study, actual age estimates were made based on dental eruption schedules and timings (Appendix IV. 1). Based on two individual *Saguinus fuscicollis*, for whom exact birth dates were known, the eruption schedule predicted by Glassman (1983) overestimated ages slightly. Therefore, exact ages were estimated to be closer to the lowest point in the age bracket predicted for each dental eruption stage. At this time, the oldest individual of known age is *ca*. 30 months old for *Saguinus fuscicollis*, and *ca*. 20 months for *Saguinus imperator*. We have accurate estimates of ages (to the month) for 15 *S. fuscicollis*, and 10 *S. imperator*. An additional yearly census of this population will both increase the robustness of further analyses, as well as the numbers of individuals with known ages, facilitating age-related analyses.

For individuals without any deciduous dentition, estimates of chronological age were not possible; however, age-class assignations were made based on occlusal wear of the mandibular first molars. Five major wear categories, with subdivisions indicating different wear patterns on the tooth, were subsumed into four age-classes – infants, young adults, adults and older adults. This method of age-class assignation relies solely on dental information, and due to the high

interindividual variability of molar wear among adults, finer age-classes were not reliably distinguishable, although attempts at doing so have been made in the past (Garber et al. 1993). We did not find the categories specified by Garber et al. (1993) corresponded chronologically with wear patterns observed at CICRA. This leads to the question of why dental wear-dependent aging is necessary at all, when previous studies (Goldizen et al. 1996; Soini & Cóppula 1981) have used physical appearance, weight, and reproductive morphology to make similar categorizations. In the case of callitrichids, reproductive suppression of juveniles or subadult individuals while in their natal groups may result in individuals with less developed genitalia and scent glands that belie their true age. Therefore, using visible characteristics of sexual maturity to assess age for individuals that are sexually suppressed could lead to underestimations of age. Molar occlusal wear might be a more accurate way to determine the age-class membership in these species.

It is important to note that although individuals in both species have been placed in the same group of age-classes, it does not signify that the adult age-classes of two species are consistent with one another. Based on the oldest individual of known age in the infant and young adult age-classes, approximations for the duration of each age-class were made, assuming equal wear rates for both species. These approximations indicate a longer lifespan for *Saguinus fuscicollis* over *Saguinus imperator*. However, because this conclusion is dependent on the proportions of individuals in each class, further sampling of the *Saguinus imperator* population could affect these numbers. Moreover, if *S. imperator* had slight diet or mastication differences that resulted in slower tooth wear patterns, it is possible that *S. imperator* and *S. fuscicollis* would share similar lifespans.

IV. 4. 1: Population Viability Analyses

A subset of all individuals in the population were monitored with two censuses, and for these individuals, transition tables that are age-class dependent were created to determine the

probabilities of individuals moving from one age-class to the next. Dental casts of several adults were obtained for a single census, but these individuals were sometimes not observed during the subsequent census. Some possible options were then evaluated for the fates of these individuals (death or dispersal), as well as models that excluded these individuals from the analyses. Overall, several general differences were observed between the two species, irrespective of the exact fate picked for these adult individuals. First, infant mortality was higher in the population of *Saguinus imperator* than in *S. fuscicollis*. Second, while only adults and older adults reproduced successfully in *S. fuscicollis*, only younger adults and adults reproduced in *S. imperator*. Third, old adult *S. imperator* survived for at least two years, whereas older adult *S. fuscicollis* experienced high mortality rate over the projection interval of a year. Using the same analyses but excluding males, we observed a significant attrition in the stable age-structure of the young adult female *Saguinus fuscicollis* (unfortunately, insufficient numbers are available for *S. imperator*). Although further analyses show no sex-bias in dispersal of individuals in this species, the attrition rate implies that more females may leave groups than are replaced by successful immigration among *S. fuscicollis* in this study period, over a relatively short period of time.

Ideally, the census interval of a year (also the projection interval in this case) ought not to be longer than any single age class. However, for *Saguinus fuscicollis*, several factors need to be considered: a) the birth season for *S. fuscicollis* is slightly earlier than that of *S. imperator*, based on further analyses, and b) we observed that individuals born in one cohort (currently in the infant age-class) would likely already be in the adult age-class when next censused ~ 12 months later. Therefore, the young adult AC appears to be necessarily < 12 months in duration for this species, resulting in in an underestimation of individuals in the young-adult AC each year, to the advantage of the adult AC instead. Had the censuses been conducted earlier, the age-distribution observed would have been slightly higher for AC young adult, and lower for AC adult. However, this was not an option given that the traps used to capture the animals function

best in the dry season, after individuals have begun to acquire their permanent dentition (Chapter III).

IV. 4. 2: Species-Specific Trends

Upon considering the possible options for adults who disappeared from the censused population, we observed trends particular to each species. *Saguinus fuscicollis* experience a short but successful infant life-stage, with a high probability of surviving to adulthood, where they remain and reproduce for quite some time. When their teeth degrade to the extent of appearing almost completely flat, they do not survive longer than a year, but continue to successfully reproduce right up to their demise. *Saguinus imperator*, on the other hand, experiences a stable infant stage, followed by a young adult stage with ~20% mortality but a 40 – 60% fecundity. They then enter an adult stage that extends for a shorter period than the adult phase in *S. fuscicollis*, where they continue to reproduce. Once they move into the older adult phase, however, despite it extending for as long as 2 years in some cases, they do not reproduce further.

These generalizations are not meant to define patterns across this species, but to compare two sympatric populations across roughly the same time period. It is certain that much can be deduced from this methodology, but that further censuses could alter the patterns described above. I present these models of transitioning from one age-class to another as an important and useful evaluation of population dynamics using pooled cross-sectional data, when longitudinal data are not available for a sufficient amount of time. Despite these caveats, these trends suggest a few future directions of study in this population. First, as the population becomes increasingly habituated to the baiting techniques used to capture them, it is possible that they would feed at the traps even during the rainy season. If this could be demonstrated, it would be advisable to shift the trapping season to earlier in the year, so as to census the population immediately after the birth of infants, which will have the important consequence of

obtaining data on the young adult age-class in both species in subsequent years. Second, if more continuous observation were possible in the months of September to March each year, important information on exact birth dates for individuals could be obtained.

As a final note, it appears that callitrichids in this population display a similar life history survivorship curve to that of other primates, with an initial drop in survivorship of infants and young adults, followed by a stable adulthood, and then a final increased mortality of older individuals (Alberts & Altmann 2003). The high rates of infant mortality appear to be countered by rates of twinning in this population, and survivorship is relatively high in the adult age classes, resulting in slight increase in numbers over time in both species at this site.

IV. 5: Chapter Summary

1. Age-structure can be predicted based on dental evaluations of molar occlusal wear and eruption timings.
2. We assume equal wear rates among species, but if *Saguinus imperator* has differing diet or masticatory patters, wear could be slower in this species.
3. A slower rate would predict roughly equal lifespans of each species, but this means that individuals currently in the younger adult age class among *Saguinus imperator* are older than those in the same age class for *S. fuscicollis*, which has important ramifications for reproduction
4. In this study population, over a relatively short timespan, we found that adults and older adults reproduce among *Saguinus fuscicollis*, but younger adults and adults reproduce among *S. imperator*, a difference that could be accounted for by the likelihood that young adult *S. imperator* are actually older than predicted by the model.
5. Given the short duration of the younger adult class among *Saguinus fuscicollis*, an ideal census interval would either be shorter or the censuses themselves conducted earlier in

the year to capture more individuals as they pass through this age-class; however, this is not always feasible given the constraints of a capture and release program.

6. Older adult *Saguinus imperator* that do not reproduce in this model are likely a product of insufficient sampling at this time and continuous monitoring might indicate that they are indeed fecund.

Appendix IV. 1A: Known ages or estimated exact ages for individuals < 1 year of age of *Saguinus fuscicollis*, organized by group. See Tables IV. 2A and IV. 2B for age-class categories.

ID	Age-range (Estimated age/Known Age) of *Saguinus fuscicollis*			
	Date	Class	Range (mo)	Estimated Age (~) or Known Age(*)
F12	11/23/09	0	0	Birth
	12/17/09	Ia	0-1½	*1 mo
	4/14/10	Ic/ 2	5¼-5¾	*4½ mo
	5/20/10	Id/2	5¾-7¼	*6 mo
	7/5/10	Ie/2	7¼-9¾	*7¼ mo
F13	11/23/09	0	0	Birth
	12/17/09	Ia	0-1½	*1 mo
	3/2/10	Ib	1½-3	* 3¼ mo
	4/14/10	Ic/ 2	5¼-5¾	*4½ mo
	5/20/10	Id/2	5¾-7¼	*6 mo
	7/5/10	Ie/2	7¼-9¾	*7¼ mo
F14	6/8/12	Ie/2	7¼-9¾	~7¼ mo
F15	6/8/12	Ie/2	7¼-9¾	~7¼ mo
F23	4/24/11	Ib	3-4½	~ 3 mo
F24	4/24/11	Ib	3-4½	~ 3 mo
M22	6/30/12	Id/2	5¾-7¼	~ 5¾ mo
M32	5/5/10	Ic	4½-5¾	~ 4½ mo
M33	5/5/10	Ic	4½-5¾	~ 4½ mo
M43	4/11/11	Id/2	5¾-7¼	~ 5¾ mo
F43	4/11/11	Id/2	5¾-7¼	~ 5¾ mo
M44	6/20/12	If/3	9¾-11¼	~ 9¾ mo
M45	6/20/12	If/3	9¾-11¼	~ 9¾ mo
M51	6/28/10	Id/2	5¾-7¼	~ 5¾ mo
	7/21/10	Id/2	5¾-7¼	~ 5¾ mo
F53	6/16/12	Ie/2	7¼-9¾	~7¼ mo
F60	6/25/12	Ie/2	9½-9¾	~9½ mo
M71	7/6/12	If/3	9¾-11¼	~ 9¾ mo
M72	7/6/12	Id/2	5¾-7¼	~ 5¾ mo

Individual IDs are assigned based on a coding system, for example F-53 can be interpreted as such: F = Female animal; 53 = Group 5, female number 3.

Estimated ages are taken as the lower of the age-bracket values for each animal, since F12 and F13 with known ages align to this pattern.

Appendix IV. 1B: Estimated exact ages for individuals < 1 year of age of *Saguinus imperator*, organized by group. See Tables IV.2A and IV. 2B for age-class categories.

ID	Age-range (Estimated age/Known Age) of *Saguinus imperator*			
	Date	Class	Range (mo)	Estimated Age (~) or Known Age (*)
M12	6/24/12	Ie/2	7¼-9¾	~ 7¼ mo
M13	6/24/12	Ie/2	7¼-9¾	~ 7¼ mo
F21	4/17/11	Ib	1½-3	~ 1½ mo
M23	4/17/11	Ib	1½-3	~ 1½ mo
F22	6/13/12	Ie/2	7¼-9¾	~ 7¼ mo
F23	6/13/12	Ie/2	7¼-9¾	~ 7¼ mo
F32	6/10/12	Ie/2	7¼-9¾	~ 7¼ mo
M33	6/10/12	Ie/2	7¼-9¾	~ 7¼ mo
F40	4/22/11	Ic/2	5¼-5¾	~ 5¼ mo
F43	4/22/11	Ic/2	5¼-5¾	~ 5¼ mo
F52	5/4/11	Id/2	5¼-5¾	~ 5¾ mo
F53	Not trapped	NA	NA	Presumed ~ 5¾ mo

Individual IDs are assigned based on a coding system, for example M-23 can be interpreted as such: M = Male animal; 23 = Group 2, male number 3.

F53 was not trapped in the first year of her birth, but was captured the next year and is most likely the twin of F52.

Chapter V: Growth and Developmental Trajectories in *Saguinus fuscicollis* and *Saguinus imperator*

V. 1: Introduction

Morphometry, or the study of the variation in the shape or size of an organism, is an important component of an integrated perspective on growth and development. It can be used to infer growth rates and outline development schedules in a species, to better understand inter- and intra-species variability in these traits. Distinguishing between shape and size can explain variation in measurements of limbs or other structures, which can subsequently explain functional differences in the use of space by different species (Falsetti et al. 1993). Variation in the genus *Saguinus* has been studied in relation to geographic chromatism, or pelage variations across river boundaries that accompany speciation by isolation (Hershkovitz 1977b), and more recently, in relation to both genetic variation (Araripe et al. 2008; Cropp 1997) and facial or cranial morphological variation between species (Cheverud 1995; Cheverud & Moore 1990; Cheverud et al. 1994). In this study, we examine if adaptive divergence in morphometrics between species is detectable in *Saguinus*, and explore the extent to which age-structure correlates with post-cranial morphological variability.

Long-term studies of primates have the advantage of known-age individuals monitored from birth, or individuals of well-estimated age evaluated on the basis of dentition and morphology (Clutton-Brock 2012; Dietz et al. 1994; King et al. 2011). In the absence of longitudinal data on wild populations, growth and development can also be analyzed via cross-sectional data from wild-caught animals (Baden et al. 2008; Hamada et al. 1986; Hamada et al. 2006; King et al. 2011), captive animals (Hamada et al. 2005), or skeletal remains (Bolter & Zihlman 2003). These cross-sectional morphometric data allow insight into subspecies or species differences, functional relations in the skeleton, and growth across age-classes. To facilitate the study of life history variables in these species, a capture and release methodology

can provide data on physiology and morphology (Glander et al. 1992; Huck et al. 2011; King et al. 2011).

V. 1. 1: Somatometric Measures

Comparative data on somatometrical measures of callitrichid species from wild-caught populations are relatively scarce in the literature; however, the morphometry of genitalia and scent glands have been described in some species. A comprehensive study of *S. fuscicollis* in Peru identified specific cutoffs for genitalia and suprapubic gland sizes that determine adulthood in each sex, and described morphological changes specific to adult individuals (Soini & Cóppula 1981). In captivity, the anatomy of the circumgenital gland of adult male and female *S. fuscicollis* was described in detail (Zeller et al. 1988), and the components of scents characterized and tested in numerous experimental conditions (Epple 1982; Epple 1981; Epple et al. 1987). A field study on *Saguinus mystax* using methodology analogous to Soini and Cóppula (1981) indicates that there are large individual differences in testicular volumes, that testicular volume is not correlated to either age-class or weight, and that genitalia size varies cyclically through the year (Garber et al. 1996). When changes in reproductive and somatic morphology are described in relation to age or age-class, behavior, seasonality or body mass, for two closely related, sympatric callitrichid species, a unique opportunity is created. Not only could one examine species or sex differences, but one could also evaluate the plasticity of each trait across the population and the individual's lifespan.

Body mass measurements in primates, have been the subject of intense study for some time (Altmann & Alberts 1987; Garber & Teaford 1986b; Smith & Jungers 1997; Terranova & Coffman 1998), and cyclical changes in the body mass of callitrichids through the year have been shown to be a factor of resource availability as well as reproductive cycles (Garber & Teaford 1986b; Sánchez et al. 2008). Since body weight is transmitted through skeletal components to a substrate, a close relationship is predicted between body mass and limb proportions (Gingerich

1990). As animals develop, the distribution of limb mass changes, for e.g. demonstrated among infant baboons (Raichlen 2005), suggesting that closely related species with different body masses might not necessarily alter their overall size, but redistribute weight through their limb segments instead.

The rate at which adult body mass is achieved could vary by species (Smith & Jungers 1997), habitat (Hamada et al. 2006), and between wild and captive individuals (Leigh 2005). Sexually monomorphic species are expected not to display differing rates of growth between the sexes, supported for example, by work on owl monkeys in Argentina (Huck et al. 2011). Locomotor differences have also been suggested as explanations for differing rates of somatic growth between species, as with crested langurs and vervet monkeys (Bolter 2011). Certain body elements can grow faster than others, with limb segments attaining adult values among wild sifakas faster than did adult body mass (King et al. 2011).

V. 1. 2: External Genitalia and Circumgenital Morphology

Male external genitalia vary in appearance across callitrichid genera, with the genus *Saguinus* possessing a cylindrical penis, tapering to an undifferentiated glans, with a well developed but not specialized baculum (as opposed to *Leontopithecus* and *Callimico*) (Hershkovitz 1977b). Testes are sessile in young, pendulous in older individuals, and can retract in situations of stress. Absolute size differences between the species are not verifiable from museum preserved specimens, but great inter-individual variation exists within species (Garber et al. 1996; Ginther et al. 2002), and season is known to affect testes size in *S. mystax* (Encarnacion et al. 1990; Garber et al. 1996). Studies of hormonal profiles of males have shown insignificant differences between breeding and nonbreeding males in *S. mystax* (Huck et al. 2005b), and that natal male *S. oedipus* (Ginther et al. 2002; Ginther et al. 2001) and *Callithrix jacchus* (Baker et al. 1999) are behaviorally and not hormonally restricted from mating in their natal groups. Female external genitalia among the callitrichids are often more pronounced than

in males, and there is inter-genera variation in terms of size and differentiation of the labia majora (Hershkovitz 1977b). The distal labia minora are enlarged into a visible, pigmented clitoris, and a hymen is present but not exposed externally.

The circumgenital area above the penis or clitoris in *Saguinus fuscicollis* is developed into a rectangular suprapubic pad (Zeller et al. 1988) that consists of apocrine and holocrine glands. This area, henceforth referred to as the suprapubic scent gland, is much more developed in females than in males (French & Cleveland 1984; Zeller et al. 1988), but is not affected either in appearance or function by castration (Epple 1982; Epple 1981). Animals rub the gland onto substrates to deposit olfactory secretions (Hershkovitz 1977b) from which individuals can discern species and subspecies differences (Epple et al. 1987), as well as information on individual identity, gender, and reproductive status (Converse et al. 1995; Epple 1979; Epple et al. 1981). Scent marking also plays a role in territoriality in the Callitrichidae (cf Roberts 2012).

V. 1. 3: Brief Study Outline

In this study, I evaluated the differences in growth and morphology between two callitrichid species, *Saguinus fuscicollis* and *S. imperator*. I use body mass and somatometric measurements from both species, which are influenced by both environmental and genetic factors, to compare these sympatric species. After accounting for pseudoreplication from multiple measurements of animals, I identify mean adult values for all measured variables for each sex of both species to address the following questions:

-Are there significant differences between body mass and limb segment lengths and circumferences between the two species? The robust appearance of *S. imperator* suggests that even though limb lengths might not be longer in this species than in *S. fuscicollis*, limb circumferences might be larger and account for their higher body masses.

-Do growth rates, evaluated by the rate of change of specific body elements of each species, differ between species? For those individuals for whom we have chronological ages

ranging from 1 to *ca*. 30 mo, does growth of these morphometric characters differ by sex or species?

-Do the genitalia and scent glands of each species differ in morphology, development, or growth over time? Are published cutoff-values for adult *S. fuscicollis* (Soini & Cóppula 1981) applicable to this study population, and if so, can similar cutoffs be determined for *S. imperator*?

-Can scoring keys for genitalia and scent glands be used to visibly evaluate age across all age categories in these species?

-Are there seasonal differences in morphological characters in these species? Are these differences then tied to ecology or reproductive biology, and what would be necessary to evaluate this question fully?

V. 2: Methods

V. 2. 1: Age-categories

Individuals were scored on the basis of molar occlusal wear, dental eruption schedules, and timings, as described in Chapter IV. Those individuals who were not captured but present in the population are excluded necessarily from this dataset. Overall, the dataset on *Saguinus fuscicollis* is more complete than that of *Saguinus imperator* due to an extra year of sampling (2009-2010); however, both species have adequate sample sizes for the statistical analysis of body mass, morphometrics and glandular and genitalia appearances: a total of 56 *S. fuscicollis* (29 females, 27 males) and 36 *S. imperator* (18 females, 18 males).

V. 2. 2: Body Mass

Body mass was measured to the nearest 10 g with a 1000 g Pesola spring-scale by placing the sedated animal in a known-weight cloth bag. Adult body mass for each sex in each species was calculated as the average of body masses of individuals in that category. Since exact chronological ages are not known in this study for adults, other methods of calculating adult body mass, such as using Gompertz curves to identify asymptotic body masses (King et al. 2011), could not be used in this study. For the adult and older adult age-classes, a percentage of individuals were measured either multiple times in a year, or over multiple years, giving rise to the problem of pseudoreplication of the data. In such cases, I took the average weight for any animal across all of its measurements within an age class, and then averaged those single values across animals to give the mean body mass for the species.

V. 2. 3: Body Measurements

Morphometric data were recorded yearly on both species of tamarins, at approximately the same time each year, which unfortunately prevents us from analyzing seasonal variation across each year. We recorded 19 standard measures on each individual (Table V. 1, Fig. V. 1). A team of two trained personnel took the measurements each year, but on some occasions, animals recovered from the anesthetic too quickly to get a complete set of measurements on

every animal. Limb segments and all circumference-measures were made with a metric tape measure to the nearest 10 mm (0.1 cm), while smaller linear measurements were recorded with a digital caliper to the nearest millimeter. Certain length measures were identified by defining landmarks on the skeleton as visible below the soft tissue, and thus, some levels of error are to be expected given the limited time available to obtain this data. To minimize this error, all measurements that could be replicated by measuring the opposite side of the body were taken and averaged. When any given side of the body was measured, and a difference > 1 cm (for length and circumference measures) or > 2 mm (for tooth measures) was observed, we repeated the measure till two consistent values could be obtained for that side of the body. Means and standard deviations are provided for all measurements per sex and age-class for each species; in some cases, due to non-normal or skewed data, generally from small sample-sizes, we observe standard deviations greater than half the mean value, which must be kept in mind during analyses.

V. 2. 4: Scent Gland and Genitalia Indices

I created index scores for phenotypic variability in scrotum, vulva and suprapubic scent-gland development in each individual tamarin of both species. Photographs of the genitalia and suprapubic glands were used to create a reliable nominal scoring system across captured individuals. Four keys were identified per species, for scrotal and vulvar development, as well as scent gland morphology for each sex (Figs. V. 2 and V. 3).

Table V. 1: Morphometrics measured on each animal

Measure	Description
Canine length*	Upper and lower canines, measured buccally, from gum to tip
Head length	Glabella of the supraorbital ridge to the occipital protuberance
Trunk length	Measured from the spine of the C1 vertebra to the base of the tail
Tail length	Measured on the ventral side from the base of the tail at the rectum to the tip of the fleshy part of the tail, excluding hair
Total body length	Sum of trunk, tail and head lengths
Upper leg length*	Lateral epicondyle of the femur to the ischial tuberosity
Lower leg length*	Lateral side of the calcaneus to the lateral epicondyle of the femur
Upper arm length*	Lateral epicondyle of the humerus to the acromion of the scapula
Forearm length*	Styloid process of the ulna to the lateral epicondyle of the humerus
Foot length*	Tip of the distal phalanx of the third digit to the calcaneus, measured separately as foot length plus the length of the digit
Hand length*	Tip of the distal phalanx of the third digit to the base of the palm, measured separately as palm length plus the length of the digit
Nail lengths*	Tip to base of the longest nail of the third digit, measured on hands and feet
Foot breadth*	Measured along the broadest part of the foot
Hand breadth*	Measured along the broadest part of the palm
Upper leg circum.*	Measured at the thickest part of the thigh
Lower leg circum.*	Measured at the thickest part of the calf
Upper arm circum.*	Measured at the thickest part of the arm
Forearm circum.*	Measured at the thickets part of the forearm
Chest circumference	Measured at the level of the sternal angle
Waist circumference	Measured at the narrowest part of the waist

*All measurements were taken on both sides of the body when possible, or on both sides of the jaw, and averaged in the dataset to minimize error.

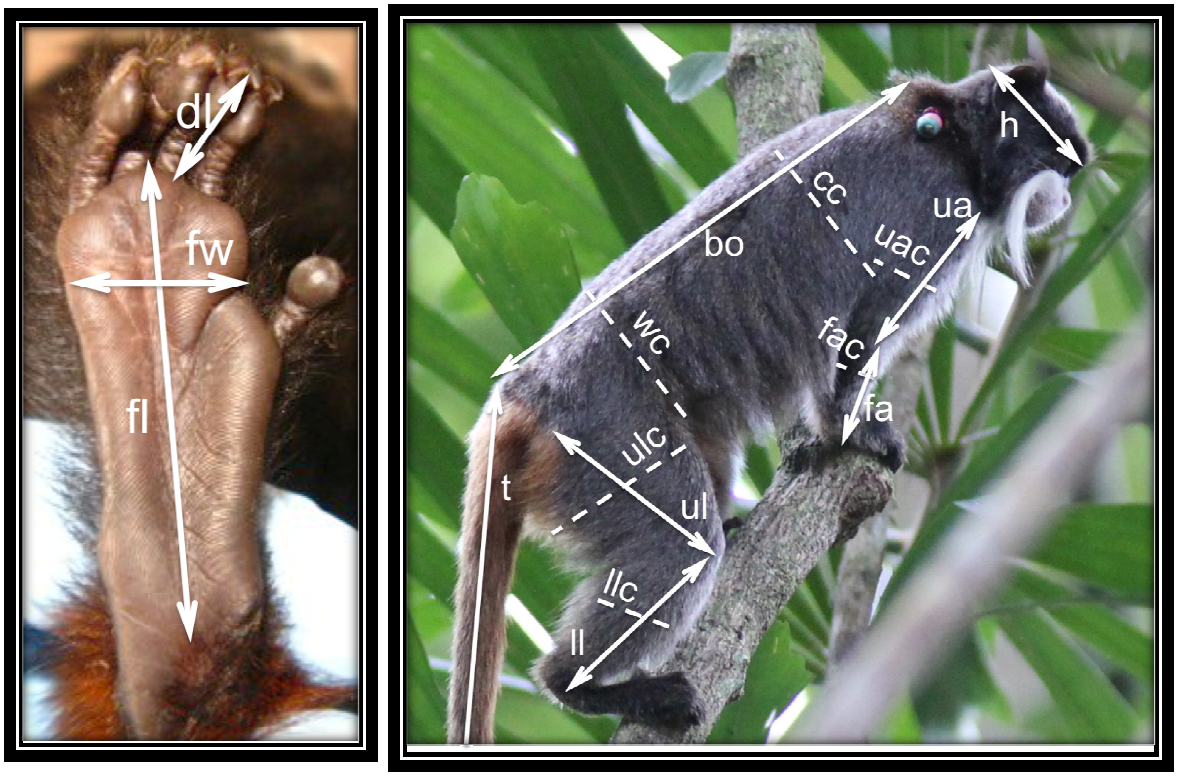


Figure V. 1A: Key to measurements taken across the body for both *Saguinus fuscicollis* and *S. imperator*. On the left is the key to foot and hand measurements, and on the right, all other body measurements. Solid lines indicate linear measurements while dotted lines indicate circumferences.

Foot and hand measurements: fw = foot or hand width; fl = foot or hand length; dl = length of the third digit on the foot or hand. Note: total foot or hand length is the summation of fl and dl. Body measurements: h = head length; ua = upper arm length; fa = forearm length; bo = trunk length; t = tail length; ul = upper leg length; ll = lower leg length; cc = chest circumference; uac = upper arm circumference; fac = forearm circumference; wc = waist circumference; ulc = upper leg circumference; llc = lower leg circumference. Note: total body length = h + bo+ t.

To create the categories for each key, each element (scent gland, vulva or scrotum) was evaluated for intensity and localization of pigmentation, as well as general shape and size. The number of categories chosen in each key is unique to each sex and species, and therefore, scores for different elements, between species or between the sexes, should not be directly compared.

The primary goal was to create scores that are each mutually exclusive from the rest in that key, so that all individuals can be reliably classified without any prior information on the age or development stage of the individual. The resulting keys (Figs. V. 2 and V. 3) contain both

archetypical photographs from each score category, as well as written descriptions highlighting the aspects that distinguish scores from each other.

V. 2. 5: Testicular Volumes and Vulvar Indices

Testes in the Callitrichidae descend just before or soon after birth, and are positioned above the pubic symphysis just under the skin; the scrotum enlarges in preparation receive these inguinal testes, that in turn expand with passage of time (Hershkovitz 1977b). Several studies have used testicular volumes to compare testes size over simple length or width measurements, and while there are multiple methods used to estimate absolute testicular volumes (cf Sakamoto et al. 2007), testicular volume was calculated in this study based on a formula first proposed for use on adolescent humans (Hansen 1952; Hansen 1949), and subsequently used on tamarins (Abbott & Hearn 1978; Garber et al. 1996; Glander et al. 1992; Soini & Cóppula 1981). It models testicles as spherical ellipsoids:

$$\text{Testicular Volume} = (\pi x y^2)/6$$

where x is the length of the testicle and y is the width of a single testicle. I measured complete testicular width (including both testicles) and divided by 2 to determine y. The vulvar index was the sum of the length and width of each vulva (as per Soini & Cóppula 1981) (see Figure V. 1B for details). Although Soini and Cóppula presented 430 mm^3 and 19 mm as thresholds for adulthood for testicular volumes and vulvar indices respectively in *Saguinus fuscicollis* (1981), I compared these volumes across age-classes that were based on dentition alone to determine appropriate thresholds, if any, for the two species in this study.

V. 2. 6: Correlating Scoring Systems with Ageing Keys

Every individual was scored for genital condition and suprapubic gland development from photographs and the keys above (Fig. V. 2. and V. 3) while keeping its identity masked, to avoid biasing the scores with knowledge of the life history of each named individual. These scores were closely examined for individuals within the Infant age-class to examine correlations

between age-class and the development of external genitalia and scent glands. A tight correlation would indicate that age was the driving feature in the developmental morphology of external genitalia and scent glands during early development; however, the converse can show that factors other than age can contribute to gland and genitalia development.

V. 2. 7: Facial and Body Morphology

Both *Saguinus fuscicollis* and *Saguinus imperator* undergo visible and distinct changes to their physical appearance from birth to subadulthood. Using photographic evidence and field observations, I attempt to correlate these changes in the physical characteristics of the face to age classes in both species. I used images of the facial hair in both species to develop a key to describe visible changes that occur during early infancy (Fig. V. 4). Then, using facial images captured during trapping as well as estimated age, I identify the approximate ages at which each morphological change occurs in both species (Fig. V. 4).

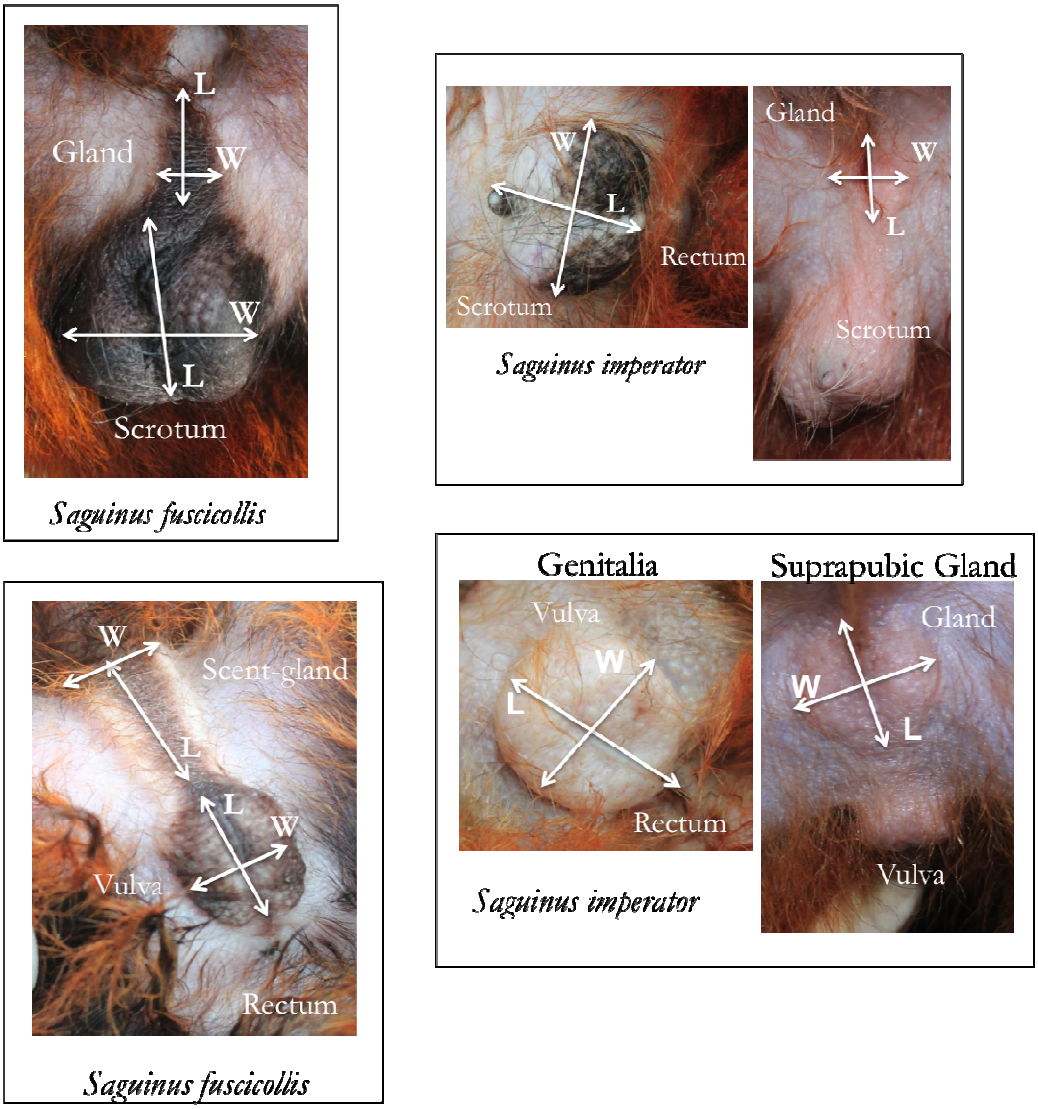


Figure V. 1B: The anatomy of genitalia and circumgenital/suprapubic gland structures in *Saguinus fuscicollis* and *S. imperator*.

Top: Scrota and suprapubic glands in males of both species

Bottom: Vulvas and suprapubic glands in females of both species

L = Length; W = Width; Arrows indicate measurement points across the widest portion of the structures. Where possible, the rectum, scrotum, vulva or gland is marked. All measurements were taken from the base of the structures.

Figure V. 2A: Key for scrotal development in *Saguinus fuscicollis*. Scores range from 1 (almost depigmented) to 5 (deeply pigmented).

Score 1	Score 2	Score 3	Score 4	Score 5
Scrotal sac white with two small patches of black, tip of the penis is dark, overall size is small	Scrotal sac is 50% pigmented, and the tip of the penis is definitely dark	Pigment lacking in random spots across a uniformly black scrotum, including the entirety of the penis	Scrotal sac completely pigmented, including he shaft of the penis	Scrotal sac beginning to get depigmented in a ring around the penis.

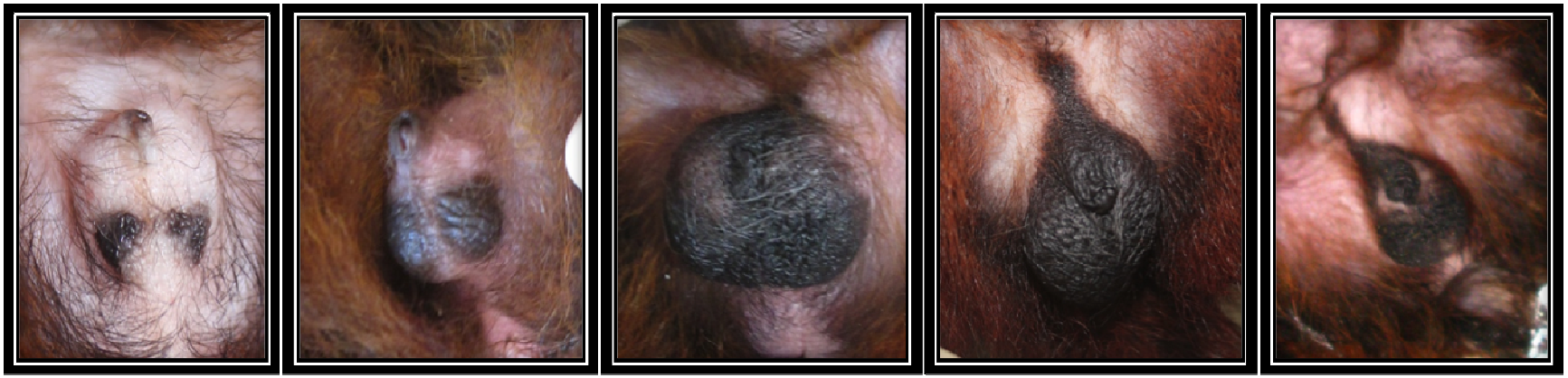


Figure V. 2B: Key for male suprapubic gland development in *Saguinus fuscicollis*. Scores range from 1 (absence of suprapubic gland) to 5 (overt suprapubic gland). A square under Score 4 indicates the location of the gland.

Score 1	Score 2	Score 3	Score 4	Score 5
No gland present whatsoever	Very slight pigmentation just above the scrotal sac	Deep pigmentation just above the scrotal sac that tapers abruptly	Deep pigmentation above the scrotal sac that tapers gradually	The gland is engorged, and deeply pigmented

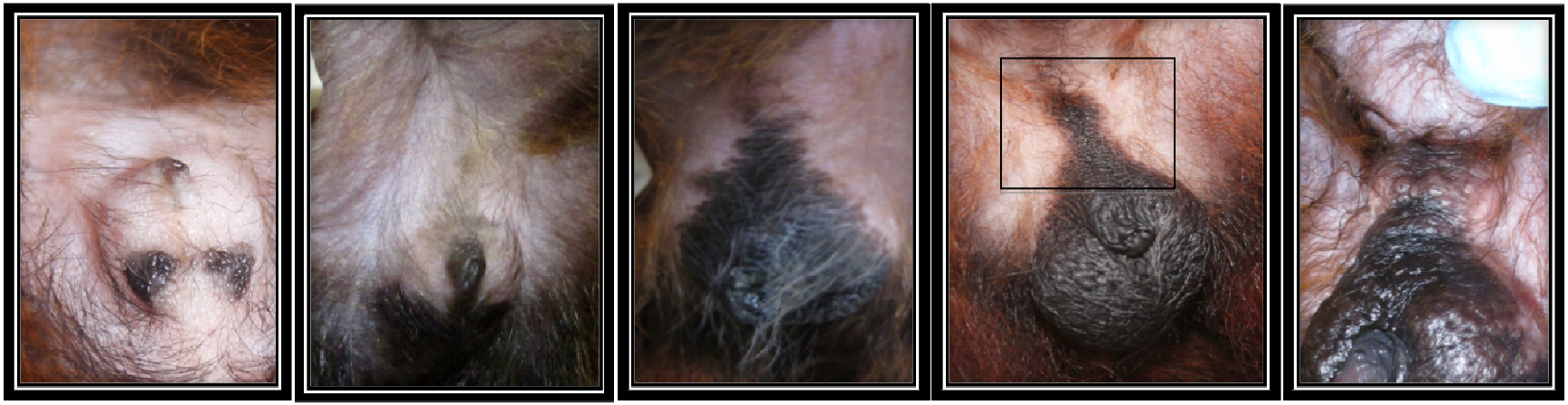
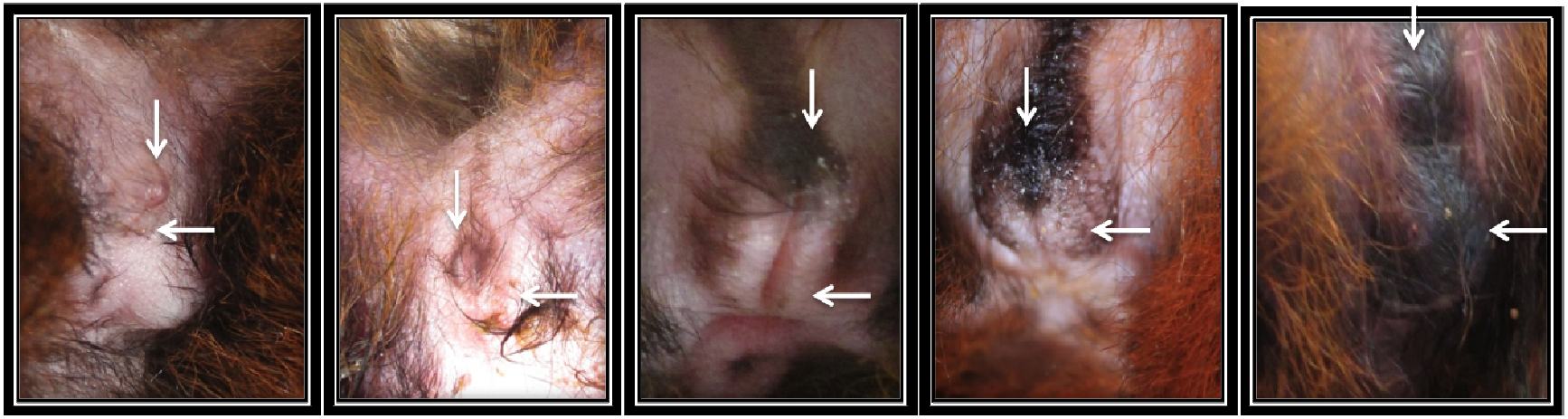


Figure V. 2C: Key for vulva development in *Saguinus fuscicollis*. Scores range from 1 (small nonpigmented vulva) to 5 (deeply pigmented vulva).

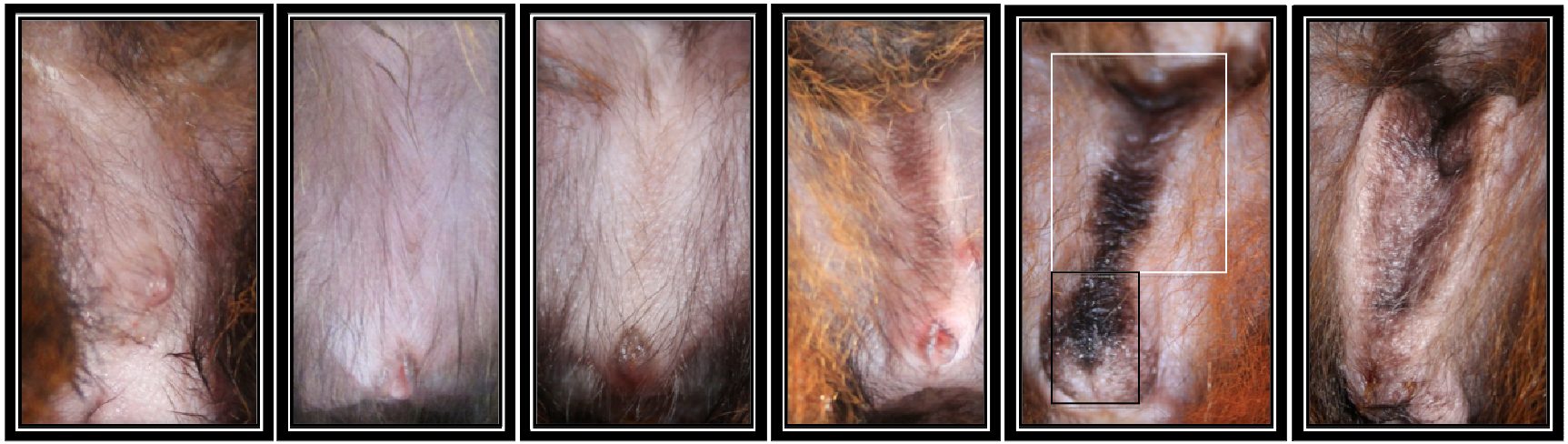
Score 1	Score 2	Score 3	Score 4	Score 5
No pigmentation at all,	The labia are slightly pigmented but the rest of the vulva is not	Slight pigmentation around the sides of the vulva, and pigmented clitoris with distinct labia	Scattered pigmentation across the vulva, pigmented clitoris and distinct labia	Completely pigmented vulva, clitoris and labia



A vertical white arrow indicates the clitoris and a horizontal arrow the labia. Refer to Fig. V.1B for further anatomical landmarks.

Figure V. 2D: Key for female suprapubic gland development in *Saguinus fuscicollis*. Scores range from 1 (absence of suprapubic gland) to 4 (overt suprapubic gland).

Score 1	Score 2	Score 3	Score 4	Score 5	Score 6
No pigment on vulva or where gland would be, only slightly formed vulva.	Gland area demarcated but clear and unpigmented, labia are slightly pigmented.	Gland streak visible, but gland not raised, labia remain pigmented.	Gland slightly raised, streak broader and clear, but still only brown pigment, labia remain unpigmented.	Streak is broad and black, gland is raised but still undefined, vulva is pigmented by this stage.	Distinctive white ridged edges on gland, strong broad pigmentation of gland.



At Score 5, the white box indicates the suprapubic gland, and the black box the vulva. For more anatomical landmarks refer to Fig. V. 1B

Figure V. 3A: Key for scrotal development in *Saguinus imperator*. Scores range from 1 (depigmented scrotum) to 6 (deeply pigmented scrotum).

Score 1	Score 2	Score 3	Score 4	Score 5
Small scrotum, barely formed, No pigmentation, but pink bumps may be present	Pigment in two distinct patches on lower half of scrotum, tip of the penis could be very slightly pigmented. Bumps visible clearly	Pigmentation covers 2/3rds of scrotal sac but a clear ring of skin around the penis still exists. Tip of penis light or slightly pigmented	Scrotal sac pigmented upto penis and/or including it	Depigmentation of scrotal sac in top half, pigmented uniformly across the bottom half, and penis still fully pigmented.

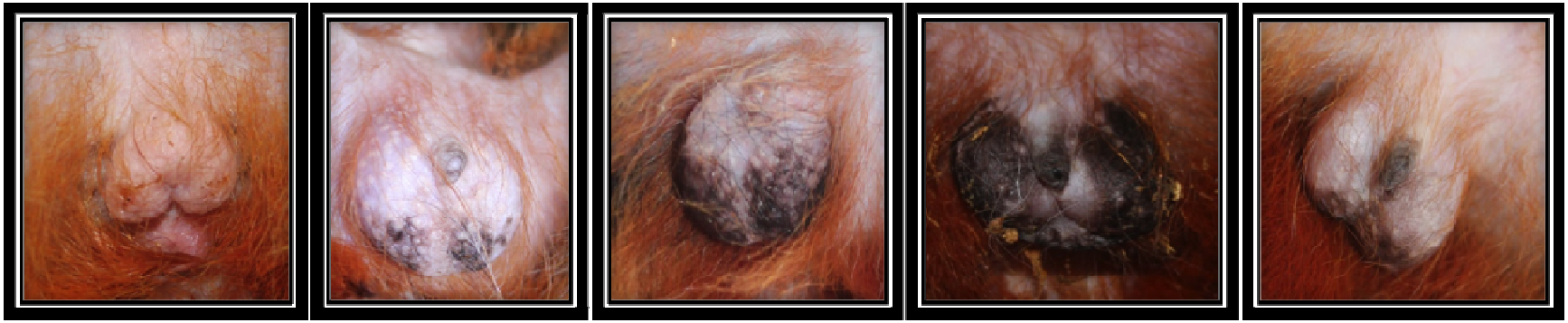
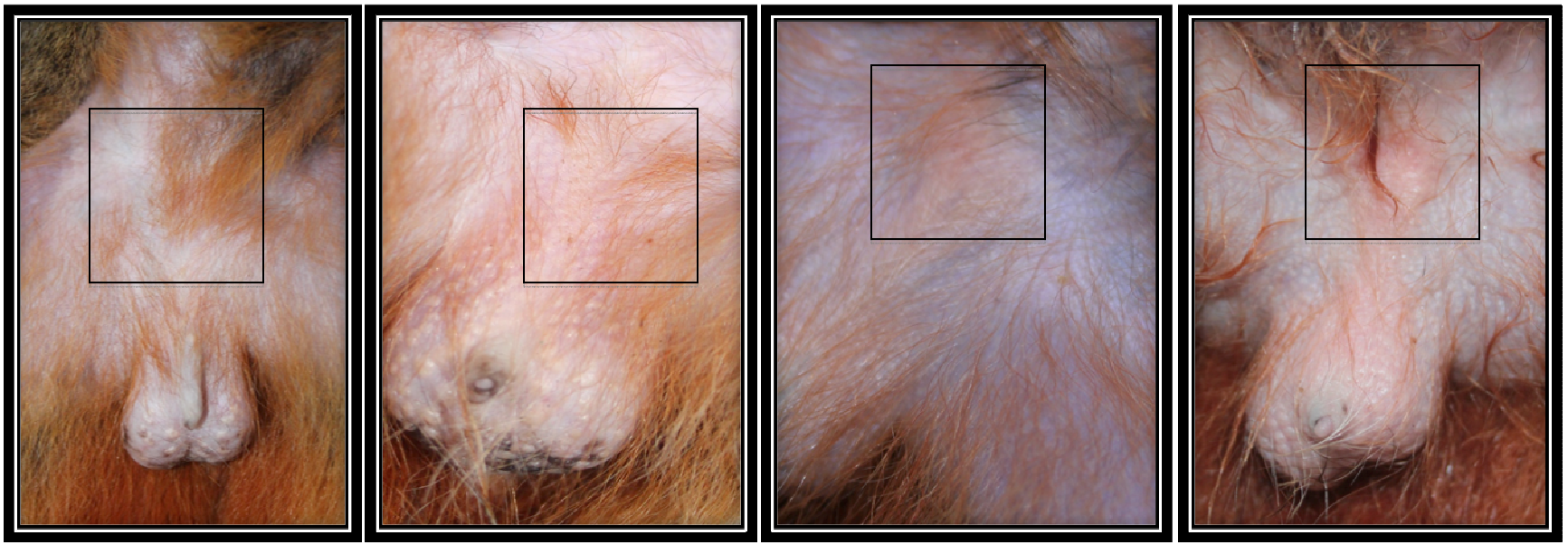


Figure V. 3B: Key for male suprapubic gland development stages in *Saguinus imperator*. Scores range from 1(absence of suprapubic gland) to 4 (raised suprapubic gland). These glands were rarely developed in males.

Score 1	Score 2	Score 3	Score 4
No gland visible at all	Gland is evidenced by slight dark orange discoloration continuous with the scrotum	The orange discoloration is pronounced, and the area is slightly raised, and is discontinuous with the scrotum	The gland is visibly raised, pinkish orange, and discontinuous with the scrotum



The location of the gland is highlighted by a box. Refer to Figure V. 1B for more anatomical detail.

Figure V. 3C: Key for vulva development in *Saguinus imperator*. Scores range from 1 (undeveloped) to 4 (overtly developed).

Score 1	Score 2	Score 3	Score 4
Vulva is small, almost triangular culminating in a small labial slit, unpigmented	Vulva is oval shaped, with a slightly larger slit, still unpigmented	Vulva is raised and spherical, with a larger, pronounced vagina	Vulva is patchily pigmented and heart shaped, culminating in the clitoris.

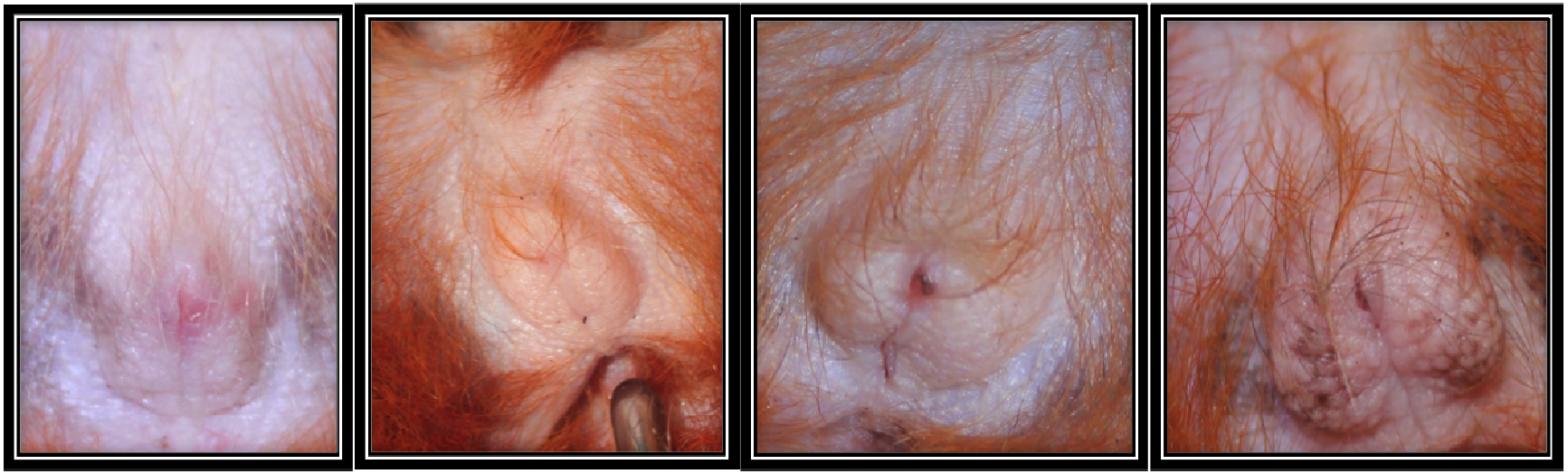


Figure V. 3D: Key for female suprapubic gland development stages in *Saguinus imperator*. Scores range from 1 (absence of suprapubic gland) to 4 (overt suprapubic gland).

Score 1	Score 2	Score 3	Score 4
No gland present at all	Gland is evidenced by slight raised pale pink-orange area, with visible bumps, not continuous with the vulva	Gland is continuous with the vulva and raised and narrow, pink in color, covered in small bumps	Gland is extremely enlarged, almost as big as the vulva itself, and is pink.

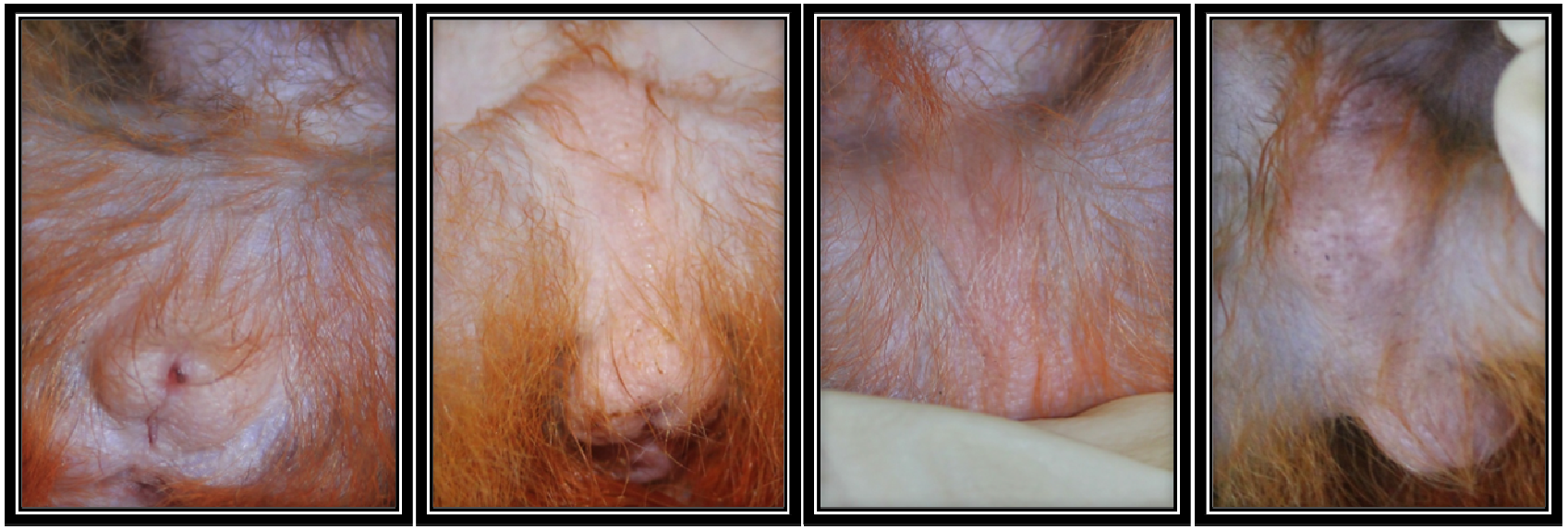


Figure V. 4A: Identification key for cheek patch development across infants in *Saguinus fuscicollis*. Scores range from 1 (most developed cheek patches in the youngest individuals) to 4 (cheek patches barely visible in an older individual).

Score 1	Score 2	Score 3	Score 4
Cheek patches large, snout mostly covered in black hair	Cheek patches large, snout mildly prognathic, white hairs beginning or present on muzzle but not as overtly as in cheek patch	Cheek patches smaller than snout, which is now white and prognathic	Cheek patches only barely visible on either side of the snout.

Figure V. 4B: Identification key for moustache and facial hair development across infants in *Saguinus imperator*. Scores range from 1 (smallest mustaches in the youngest individuals) to 4 (fully developed mustaches in an older individual).

Score 1	Score 2	Score 3	Score 4
Small tufts of mustache, undeveloped eye patches, flat face and very slight pink areas visible near the nose and mouth	Snout still only very slightly prognathic, mustaches longer but not curved, small pink area covering nose and mouth, eye patch is now blacker and more developed	White curved mustache and visible white beard, black eye patch fully developed, snout clearly outlined in pink and prognathic	Mustache is thick, long and curved, black eye patches are distinct, beard is long and straight, and the snout is clearly outlined in pink.

V. 2. 8: Data Analyses

Each measurement, including body mass, taken for an individual was compared per sex within each species, for the adult and older adult age-classes. If there were no significant differences (Mann Whitney U test, $\alpha = 0.05$), then values for the two age-classes were pooled and means calculated. These means were considered the adult mean value for the group. I compared these adult mean values for each variable measured (Table V. 1) between the sexes within a species, as well as between males and females of either species. I also looked at overall mean values for all morphometric variables with the sexes pooled for overall differences between the species. To account for multiple comparisons across each group, I adjusted the p-values using a variety of methods, including the "holm"(Holm 1979), "hochberg" (Hochberg 1988), "hommel" (Hommel 1988), bonferroni, and "BH" (Benjamini & Hochberg 1995), thus accounting for false discovery rates.

V. 3: Results

V. 3. 1: Adult Body Mass across Species and Age-Classes

There was no significant difference between the mean body weights of males in adult and older adult age-classes for either *Saguinus fuscicollis* or *S. imperator* (Mann-Whitney *U*: $P > 0.05$) (Table V. 2). The same held true for female weights between the two age-classes for both species. Therefore, for both species, we calculated adult body mass as the mean body mass of individuals in the adult and older-adult age-classes combined for each sex. Our dataset included one known female *S. fuscicollis* in the first month of pregnancy, with a slight possibility of other females in the same situation included in data from 2012. This should not significantly affect any body measurements (specially weight) given that the pregnancies are just beginning (See Chapter VI).

Table V. 2: Average body mass across age-classes in *Saguinus fuscicollis* and *S. imperator*, with a view of finer age categories for the infant age class.

Species	Mean body mass ± SD (N)							
	Infant (Ia) (0 – 1½ mo)	**Infant (Ib) (1½ – 3 mo)**	**Infant (Ic) (4½ – 5¾ mo)**	**Infant (Id) (5¾ – 7¼ mo)**	**Infant (Ie) (7¼ – 9¾ mo)**	**Young Adult**	**Adult**	**Old Adult**
Saguinus fuscicollis Females	55 ± 0 (2)	153 ± 16 (3)	210 ± 7 (2)	247 ± 18 (3)	248 ± 39 (6)	475 (1)	394 ± 31 (27)	413 ± 19 (3)
Saguinus fuscicollis Males	Unknown	Unknown	202 ± 52 (3)	220 ± 30 (4)	Unknown	270 ± 10 (3)	388 ± 32 (28)	395 ± 58 (3)
Saguinus fuscicollis (pooled sexes)	55 ± 0 (2)	153 ± 16 (3)	205 ± 37 (5)	231 ± 27 (7)	248 ± 39 (6)	321 ± 103 (4)	391 ± 31 (55)	404 ± 40 (6)
Saguinus imperator Females	Unknown	200 (1)	295 (1)	290 (1)	278 ± 8 (3)	575 ± 101 (4)	531 ± 67 (11)	618 ± 25 (2)
Saguinus imperator Males	150 (1)	Unknown	Unknown	Unknown	245 ± 22 (3)	538 ± 96 (2)	487 ± 42 (11)	508 ± 72 (4)
Saguinus imperator (pooled sexes)	150 (1)	200 (1)	295 (1)	290 (1)	262 ± 23 (6)	563 ± 92 (6)	510 ± 60 (22)	544 ± 80 (6)

N = sample size

There was no significant difference in the adult body masses between the sexes of *Saguinus fuscicollis* (395 ± SD 30 g females vs. 385 ± SD 35 g males, $P \geq 0.05$), or *S. imperator* (533 ± SD 79 g females vs. 495 ± SD 45 g males, $P \geq 0.05$). However, male and female *S. fuscicollis* differed significantly in adult body mass from those of *S. imperator* ($P \leq 0.05$), and overall adult body mass (with sexes pooled) was significantly higher in *S. imperator* (511 ± SD 63 g) than it was in *S. fuscicollis* (390 ± SD 32 g, $P \leq 0.05$) (Table V. 2).

V. 3. 1. 1: Age-effects on Body Mass

Based on individuals for whom known ages are available, I observed male and female *Saguinus fuscicollis* attain mean adult body masses at *ca*. 17 mo of age. At *ca*. 6 mo, females have attained *ca*. 63% of adult weight, and males *ca*. 57% of adult weight (Fig. V. 5A). This slightly faster, although not significantly different, body size maturation rate of females over males is observed in *S. imperator* as well, with females attaining 52% and males 50% of adult body mass at *ca*. 7 mo of age.

There were significant differences between the age-classes in terms of body mass, as expected, for both *Saguinus fuscicollis* (Kruskal-Wallis *H:* $P \leq 0.001$) and *S. imperator* ($P \leq 0.001$) (Table V. 2). In general, *Saguinus imperator* achieved mean adult weights faster overall (Fig. V. 5B). However, due to one less year of sampling with this species, we do not have sufficient numbers of infants to get precise body mass values within the different age categories, which explain certain inconsistencies such as infants in the Ie class weighing less than those in Ic, as well as what appears to be a sudden jump in weight from infant to young adult age-classes (Fig. V. 5B).

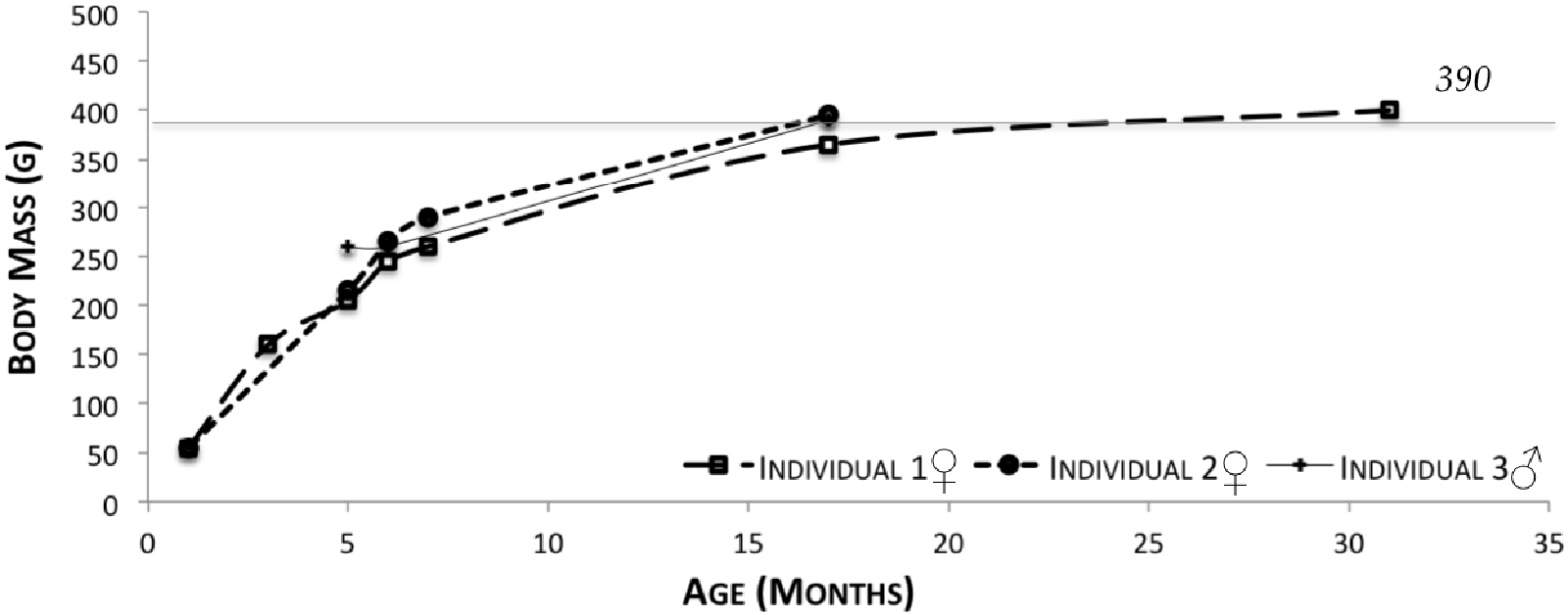


Figure V. 5A: Body mass distribution across three individuals of *Saguinus fuscicollis* for whom chronological age is known. The average adult weight is noted at *ca*. 390 g. Data on *S. imperator* is not presented because only two data points are available for any individual measured more than once at this time.

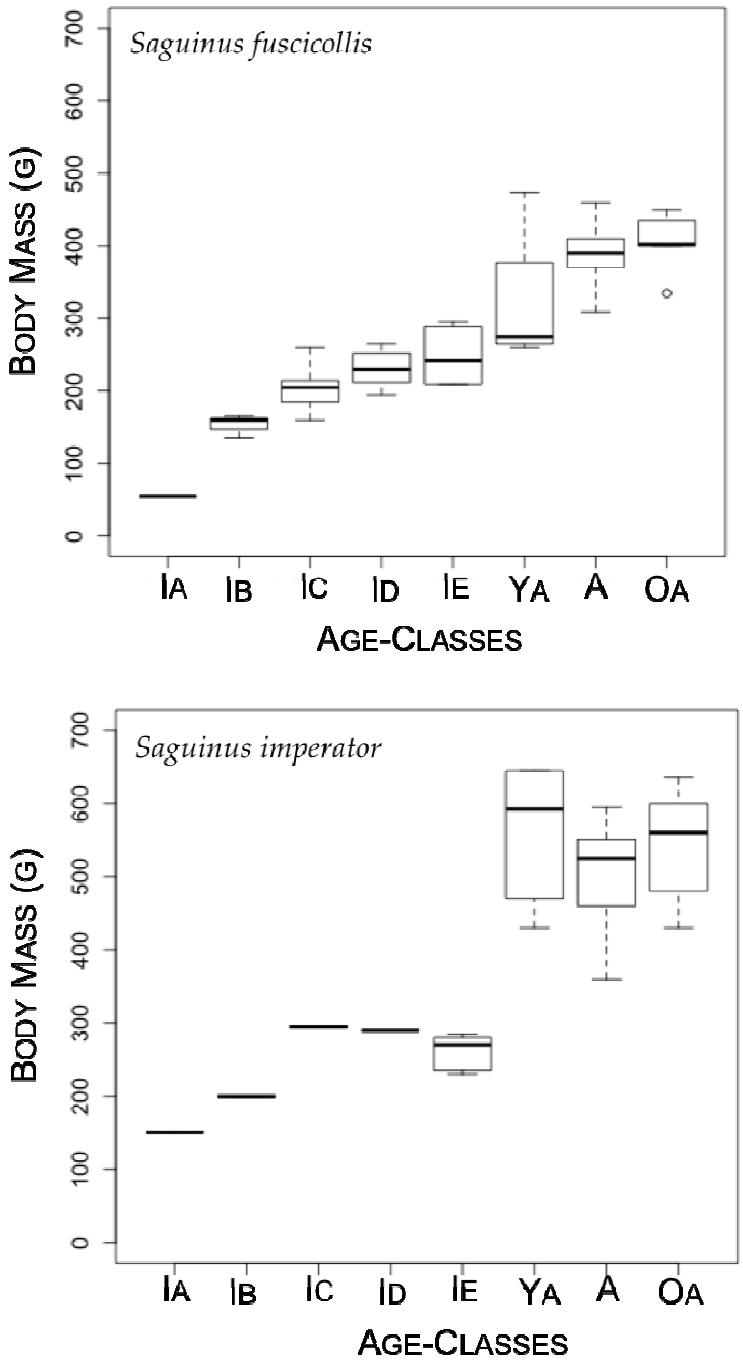


Figure V. 5B: Body mass distribution across the age-classes for both species.

Infant age-classes are subdivided further as follows: I_A (0-1½ mo), I_B (1½-3 mo), I_C (4½-5¾ mo), I_D (5¾-7¼ mo), I_E (7¼-9¾ mo). Adult classes include YA (young adults), A (adults), and OA (old adults).

In the first three months of life, infant body mass of *Saguinus fuscicollis* increased to *ca*. 153 g, and by 6 months of age, infants weighed *ca*. 230 g i.e. a 50% increase in weight (Table V. 2). At *ca*. 12 mo of age, as a young adult, they reach *ca*. 320 g, which is only a 40% increase, as growth begins to slow down. Body masses of *S. imperator* increased to *ca*. 200 g at 3 mo, and subsequently by 45% to *ca*. 290 g at 6 mo of age. Subsequently, at 12 mo of age, young adult *Saguinus imperator* achieve a weight of *ca*. 563 g, which is a 92% increase from levels at 6 mo of age (Table V. 2). Although more data will increase the confidence of this conclusion, it appears that *S. imperator* grows faster consistently throughout childhood to attain an eventual higher body mass than *S. fuscicollis*.

V. 3. 2: Body Measurements Across Species and Age-Classes

No significant differences were observed in mean values of any measurement (Table V. 1) between adult and old adult age-classes for either sex of either species; therefore, values for these two age-classes were pooled to calculate the mean adult value for each morphometric variable (Table V. 3). I corrected *P*-values to account for increased Type I errors during multiple comparisons of variables within the same dataset, and consider two means as being significantly different from each other if the *P*-value is below the alpha-level consistently using all methods. If any single method stands out as the only corrected value > 0.05, then these results are reported as well (Table V. 4).

V. 3. 2. 1: Species and Sex Effects on Morphometrics

Male and female adult *Saguinus fuscicollis* display no significant sexual dimorphism based on any of the morphometric measures but upper arm lengths, where females appear to have longer upper arms (Table V. 4). Similarly, male and female *S. imperator* show no dimorphism on any measure, except for waist circumferences. Neither upper arm nor waist circumference measures are significantly different between species with sexes pooled (Table V. 4). Although there do not appear to be many differences between sexes for either species, *S. fuscicollis* and *S. imperator* are significantly different from each other in many respects (Table V. 4). Upper, but not lower, canines are significantly longer in *S. imperator* than *S. fuscicollis*, between sexes as well as overall. While head lengths are not significantly different between the species, the trunk, tail and subsequently, total body lengths, were significantly higher in *S. imperator* than *S. fuscicollis*; in fact, female and male values for *S. imperator* are higher than the corresponding sexes in *S. fuscicollis*. None of the limb lengths are significantly different between species; however, circumferences of the arm, forearm, and lower leg are significantly higher in *S. imperator* than *S. fuscicollis* overall, and higher in both sexes independently as well (Table V. 3). Interestingly, while *S. imperator* has significantly wider feet and hands than *S. fuscicollis*, nails on the feet and hands of *S. fuscicollis* are anywhere from 1.5 to 2 times longer than those of *S. imperator*. This result applies when males and females are compared between species as well.

Table V. 3: Mean morphometric values (mean± SD mm) per sex and with pooled sexes for both *Saguinus fuscicollis* and *S. imperator*. Sample sizes in parentheses. All measures are lengths, unless otherwise specified.

Morphometric Trait	*Saguinus fuscicollis*			*Saguinus imperator*		
	Males	**Females**	**Sexes Pooled**	**Males**	**Females**	**Sexes Pooled**
Upper canine	5.0 ± 0.6 (20)	5.1 ± 0.4 (26)	5.0 ± 0.5 (46)	5.8 ± 0.8 (12)	5.9 ± 0.7 (9)	5.8 ± 0.8 (21)
Lower canine	4.3 ± 1.1 (20)	4.5 ± 0.4 (26)	4.4 ± 0.8 (46)	4.77 ± 0.3 (12)	4.8 ± 0.6 (9)	4.8 ± 0.4 (21)
Head	43.6 ± 4.3 (19)	43.2 ± 7.2 (23)	44.4 ± 6.0 (42)	44.8 ± 3.0 (12)	44.0 ± 4.1 (9)	44.4 ± 3.4 (21)
Tail	310 ± 14 (20)	323 ± 19 (24)	317 ± 18 (44)	352 ± 10 (12)	363 ± 15 (9)	357 ±14 (21)
Trunk	183 ± 18 (19)	184 ± 14 (24)	188 ±15 (43)	190 ± 10 (11)	201 ± 10 (9)	195 ± 11 (20)
Total body	533 ± 30 (18)	552 ± 25 (24)	544 ± 29 (42)	586 ± 16 (11)	608 ± 23 (9)	596 ± 22 (20)
Upper leg	75 ± 5 (18)	80 ± 5 (25)	77± 5 (43)	76 ± 4 (12)	78 ± 4 (9)	77 ± 4 (21)
Lower leg	77 ± 4 (19)	78 ± 6 (25)	78 ± 5 (44)	77 ± 3 (12)	80 ± 3 (10)	78 ± 4 (22)
Upper arm	59 ± 3 (19)	63 ± 3 (24)	61 ± 4 (43)	60 ± 4 (12)	63 ± 2 (9)	61 ± 3 (21)
Forearm	57 ± 3 (19)	58 ± 3 (24)	58 ± 31 (43)	55 ± 2 (12)	59 ± 3 (9)	56 ± 3 (21)
Foot	55.7 ± 2.9 (19)	55.4 ± 3.2 (25)	55.5 ± 3.0 (44)	56.8 ± 2.1 (12)	57.2 ± 3.6 (10)	57.0 ± 2.8 (22)
Hand	41.0 ± 1.2 (19)	40.7 ± 3.1 (25)	40.8 ± 2.4 (44)	43.0 ± 3.1 (12)	57.2 ± 3.6 (10)	42.9 ± 2.6 (21)
Hand nail	4.0 ± 0.5 (17)	4.1 ± 0.5 (23)	4.1 ± 0.5 (40)	2.9 ± 0.2 (12)	2.7 ± 0.5 (9)	2.8 ± 0.3 (21)
Foot nail	4.2 ± 0.3 (16)	4.2 ± 0.6 (23)	4.2 ± 0.5 (39)	2.8 ± 0.5 (12)	2.9 ± 0.4 (9)	2.9 ± 0.4 (21)
Foot breadth	13.4 ± 1.3 (17)	13.2 ± 1.9 (25)	13.3 ± 1.6 (42)	14.9 ± 1.5 (12)	15.4 ± 0.5 (9)	15.1 ± 1.2 (21)
Hand breadth	11.7 ± 0.8 (19)	11.3 ± 1.1 (25)	11.4 ± 1.0 (44)	14.6 ± 1.0 (12)	14.9 ± 0.8 (9)	14.7 ± 0.9 (21)
Upper leg circum.	84 ± 8 (19)	82 ± 5 (25)	83 ± 6 (44)	89 ± 7 (12)	86 ± 7 (9)	88 ± 7 (21)
Lower leg circum.	52 ± 4 (19)	50 ± 4 (25)	51 ± 4 (44)	56 ± 5 (12)	56 ± 4 (9)	56 ± 4 (21)
Upper arm circum.	54 ± 4 (19)	54 ± 4 (24)	54 ± 4 (43)	61 ± 3 (12)	61 ± 5(9)	61 ± 4 (21)
Forearm circum.	43 ± 4 (19)	42 ± 4 (28)	43 ± 4 (43)	55 ± 3 (12)	53 ± 4 (9)	54 ± 3 (21)
Chest circum.	137 ± 10 (19)	138 ± 11 (24)	138 ± 10 (43)	140 ± 11 (12)	148 ± 9 (9)	143 ± 11 (28)
Waist circum.	110 ± 20 (19)	109 ± 20 (25)	109 ± 20 (44)	99 ± 7 (12)	118 ± 13 (9)	107 ± 14 (21)
Vulvar index	-	20.3 ± 4.0 (25)	-	-	23.4 ± 6.0 (9)	-
Testicle (mm^3)	884.5±272(20)	-	-	772.0±216 (12)	-	-
Nipple	-	1.9 ± 2.1 (21)	-	-	2.5 ± 2.4 (9)	-
Suprapubic area(mm^2)	117.1±72.4 (16)	267.5± 143(25)	208.8±140(41)	81.9 ± 69.4 (9)	156.5 ±112 (9)	119.2 ± 98 (18)

Table V. 4: Results of Mann-Whitney *U* Tests on mean morphometrics between different groups. All P-values were corrected for multiple comparisons, and only significant test results are displayed here.

	SF ♂ vs. ♀	**SI ♂ vs. ♀**	**SF ♂ vs. SI ♂**	**SF ♀ vs. SI ♀**	**SF vs. SI**
Body mass (g)	-	-	$P \leq 0.001$	$P \leq 0.05$	$P \leq 0.001$
Upper canine	-	-	$P \leq 0.05$**	$P \leq 0.05$	$P \leq 0.001$
Tail	-	-	$P \leq 0.001$	$P \leq 0.05$	$P \leq 0.001$
Trunk	-	-	-	$P \leq 0.05$*	$P \leq 0.05$ *
Total body	-	-	$P \leq 0.001$	$P \leq 0.05$	$P \leq 0.001$
Upper arm	$P \leq 0.05$	$P \leq 0.05$**	-	-	-
Forearm	-	-	$P \leq 0.05$**	-	-
Hand	-	-	-	-	$P \leq 0.05$*
Hand nail	-	-	$P \leq 0.001$	$P \leq 0.001$	$P \leq 0.001$
Foot nail	-	-	$P \leq 0.001$	$P \leq 0.05$	$P \leq 0.001$
Foot breadth	-	-	$P \leq 0.05$**	$P \leq 0.05$	$P \leq 0.001$
Hand breadth	-	-	$P \leq 0.001$	$P \leq 0.001$	$P \leq 0.001$
Lower leg circum.	-	-	$P \leq 0.005$*	$P \leq 0.05$	$P \leq 0.001$
Upper arm circum.	-	-	$P \leq 0.001$	$P \leq 0.05$*	$P \leq 0.001$
Forearm circum.	-	-	$P \leq 0.001$	$P \leq 0.05$	$P \leq 0.001$
Waist circum.	-	$P \leq 0.05$	-	-	-
Suprapubic area (mm^2)	$P \leq 0.05$	-	-	-	-

SF = *Saguinus fuscicollis*; SI = *Saguinus imperator*; The last column compares the two species with sexes pooled.

* All corrected p-values but the bonferroni corrected value were ≤ 0.05

** only the BH (Benjamini & Hochberg 1995) correction showed a significant difference

V. 3. 2. 2: Age-effects on Morphometrics

The analysis of age-class effects on morphometrics is hindered somewhat by rapidly changing values during early development, prompting a finer scale within the infant class, and the subsequently insufficient number of subjects available at each individual division of the infant age-class. However, several general conclusions about the rate of growth of various variables between both species may be made (Tables V. 5A – 5F).

Comparisons of morphometrics of young individuals of known ages (at 3, 6 and *ca*. 18 mo), despite smaller sample sizes, can reveal rates of development to adulthood (Table V. 6). Canine lengths are at *ca*. 40% of full adult length by 3 mo of age, and achieve full growth by at least *ca*. 1.5 yr of age. Tail, trunk, total body, and limb lengths have reached *ca*. 70% of their full potential at 3 mo of age, while limb circumferences have only achieved *ca*. 60% of adult values at this age. However, at *ca*. 1.5 yr of age, body and limb lengths have reached their adult values, but some circumferences are increasing at slightly slower rates. Foot and hand dimensions also grow rapidly by 3 mo, and achieve their maximum values by *ca*. 1.5 yrs of age (Table V. 6).

Table V. 5A: Mean values of each morphometric value across age-classes for female *Saguinus fuscicollis*.

	Infant (Ia) (0-1½ mo)	Infant (Ib) (1½-3 mo)	Infant (Ic) (4½-5¾ mo)	Infant (Id) (5¾-7¼ mo)	Infant (Ie) (7¼-9¾ mo)	Young Adult	Adult	Old Adult
Upper canine	Unknown	1.8±0.4 (3)	2.1±0.6 (2)	2.0±0.1 (3)	2.3±0.2 (6)	5.3 (1)	5.1 ± 0.3 (23)	4.6 ± 0.6(3)
Lower canine	Unknown	1.7±0.3 (3)	2.0±0.1 (2)	1.9 ±0.4 (3)	2.0±0.3(6)	4.4 (1)	4.5 ± 0.4 (23)	4.3 ± 0.4(3)
Head	Unknown	40.9±8 (3)	39.0±5.7(2)	35.4±0.4(3)	38.7±2.0(6)	45.0(1)	43.5 ± 7.3 (20)	41.4±7.0(3)
Tail	Unknown	233 ± 3(3)	270 ± 7 (2)	288 ± 2 (3)	286 ± 16(6)	330 (1)	321 ± 17 (21)	339±29(3)
Trunk	Unknown	114 ± 5(3)	145 ± 14 (2)	164 ± 4 (3)	161 ± 12 (6)	187 (1)	183 ± 14 (21)	189±8(3)
Total body	Unknown	388 ± 8(3)	454 ± 1 (2)	487 ± 5 (3)	486 ± 24(6)	562 (1)	549 ± 24 (21)	570±35(3)
Upper leg	Unknown	48 ± 7(3)	60 ± 4 (2)	67 ± 1 (2)	63 ± 4 (6)	74 (1)	79 ± 5 (22)	82 ± 6 (3)
Lower leg	Unknown	54 ± 4(3)	62 ± 0 (2)	74 ± 4 (2)	69 ± 4 (6)	85 (1)	77 ± 6 (22)	84 ± 4 (3)
Upper arm	Unknown	39 ± 3(3)	46 ± 2 (2)	56 ± 8 (2)	51 ± 3 (6)	67 (1)	63 ± 3 (21)	64 ± 1 (3)
Forearm	Unknown	36 ± 5(3)	45 ± 0 (2)	55 ± 7 (2)	49 ± 2 (6)	65 (1)	58 ± 3 (21)	63 ± 1 (3)
Foot	Unknown	47.2±3.1(3)	56.3±1.0(2)	49.4±4.8(2)	51.8±2.9(6)	51(1)	55.3 ± 3.2 (22)	56.1±3.5(3)
Hand	Unknown	32.6±1.8(3)	35.5±1.6(2)	32.6±1.8(2)	35.5±2.0(6)	35.2(1)	40.3 ± 3.1 (22)	43.2±0.5(3)
Hand nail	Unknown	3.0±0.4 (2)	4.3±0.3 (2)	3.6±0.6 (2)	3.9 ±0.7 (6)	4.9 (1)	4.1 ± 0.5 (20)	4.3± 0.2 (3)
Foot nail	Unknown	3.0 ±0.1 (2)	4.1 ±0.3 (2)	4.0± 0.6 (2)	4.1± 0.6 (6)	4.9 (1)	4.2 ± 0.6 (20)	4.8±0.8 (3)

Table V. 5A. ***Continued***

	Infant (Ia) (0 – 1½ mo)	Infant (Ib) (1½ – 3 mo)	Infant (Ic) (4½ – 5¾ mo)	Infant (Id) (5¾ – 7¼ mo)	Infant (Ie) (7¼ – 9¾ mo)	Young Adult	Adult	Old Adult
Foot breadth	Unknown	10.7±1.1(3)	13.1 ±0 (2)	13.3±0.4(2)	12.0±0.8(6)	14.3 (1)	13.1 ± 2.0 (22)	14.0±0.6(3)
Hand breadth	Unknown	9.8±0.6(3)	12.1 ±0 (2)	9.9 ± 1.4(2)	11.5± 1.6(6)	14.7 (1)	11.2 ± 1.1 (22)	12.1±0.8(3)
Thigh circum.	Unknown	48 ± 7 (3)	65 ± 7 (2)	76 ± 7 (2)	70 ± 5 (6)	96 (1)	82 ± 5 (26)	82 ± 6 (3)
Calf circum.	Unknown	34 ± 3 (3)	42 ± 4 (2)	47 ± 1 (2)	43 ± 4 (6)	55 (1)	49 ± 4 (22)	51 ± 4 (3)
Arm circum.	Unknown	39 ± 3 (3)	43 ± 1 (2)	52 ± 5 (2)	44 ± 2 (6)	64 (1)	55 ± 4 (21)	52 ± 1 (3)
Forearm circum.	Unknown	36 ± 5 (3)	34 ± 5 (2)	46 ± 2 (2)	38 ± 3 (6)	52 (1)	42 ± 4 (21)	43 ± 1 (3)
Chest circum.	Unknown	99 ± 8 (3)	112±10(2)	127 ± 8 (3)	113 ± 13 (6)	142 (1)	138 ± 11 (21)	140 ± 15 (3)
Waist circum.	Unknown	70 ± 5 (3)	95 ± 14(2)	118 ± 32(3)	88 ± 17 (6)	110 (1)	109 ± 21 (22)	109 ±14 (3)
Vulvar index	Unknown	9.1±0.2(3)	12.2±0.1(2)	10.3±2.5(3)	10.7 ± 1.4(6)	28.1 (1)	19.8 ± 3.9(22)	24.5±2.4(3)
Nipple	0 ± 0 (2)	0 ± 0 (3)	0 ± 0 (2)	0 ± 0 (3)	0 ± 0 (6)	0 (1)	1.4 ± 2.0 (19)	4.2 ± 0.3(3)
Gland area (mm^2)	Unknown	0 ± 0 (2)	0 ± 0 (2)	78.4±25.2(3)	29.3±26.3(6)	483.5(1)	262.7±148.9(22)	302.1±99.9(3)

Table V. 5B: Mean values of each morphometric value across age-classes for male *Saguinus fuscicollis*.

	Infant (Ia) (0-1½ mo)	Infant (Ib) (1½-3 mo)	Infant (Ic) (4½-5¾ mo)	Infant (Id) (5¾-7¼ mo)	Infant (Ie) (7¼-9¾ mo)	Young Adult	Adult	Old Adult
Upper canine	Unk.	Unk.	2.4 ± 0.7 (3)	2.0 ± 0.2 (4)	Unknown	0 ± 0 (1)	5.1 ± 0.5 (19)	4.8 ± 1 (3)
Lower canine	Unk.	Unk.	2.3 ± 0.5 (3)	1.9 ± 0.1 (4)	Unknown	2.1 ± 0 (1)	4.3 ± 1.2 (21)	4.2 ± 0 (3)
Head	Unk.	Unk.	35.9 ± 2.0(3)	36.8±3.8(4)	Unknown	41.3±0.9(3)	43.6 ± 4.5 (17)	43.1±0.4(3)
Tail	Unk.	Unk.	263 ± 6 (3)	275 ± 15 (4)	Unknown	299 ± 8 (3)	311 ± 14 (17)	302 ± 10(3)
Trunk	Unk.	Unk.	130 ± 21 (3)	148 ± 5 (4)	Unknown	157 ± 5 (3)	183 ± 18 (17)	188 ± 18 (2)
Total body	Unk.	Unk.	429 ± 29 (3)	460 ± 21 (4)	Unknown	497 ± 12(3)	536 ± 31 (15)	520 ± 32(3)
Upper leg	Unk.	Unk.	55 ± 6 (3)	60 ± 1 (4)	Unknown	70 ± 3 (3)	75 ± 5 (15)	76 ± 10 (3)
Lower leg	Unk.	Unk.	57 ± 5 (3)	67 ± 6 (4)	Unknown	70 ± 2 (3)	77 ± 4 (16)	76 ± 6 (3)
Upper arm	Unk.	Unk.	44 ± 7 (3)	49 ± 3 (4)	Unknown	54 ± 3 (3)	59 ± 3 (16)	61 ± 3 (3)
Forearm	Unk.	Unk.	46 ± 8 (3)	48 ± 4 (4)	Unknown	50 ± 1 (3)	57 ± 3 (16)	57 ± 3 (3)
Foot	Unk.	Unk.	47.0 ± 6.7(3)	50.5± 1.9(4)	Unknown	54 ± 2 (3)	56.5 ± 2.5 (16)	51.8± 1.7(3)
Hand	Unk.	Unk.	31.9 ± 2.2(3)	36.8±0.8(4)	Unknown	39 ± 1 (3)	40.8 ± 1.2(16)	41.8±0.7(3)
Hand nail	Unk.	Unk.	3.9 ± 0.6 (3)	3.9± 0.6 (4)	Unknown	3.3 ± 0.5(3)	4.0 ± 0.5 (14)	4.1 ± 0.7 (3)
Foot nail	Unk.	Unk.	4.1 ± 0.6 (3)	3.7 ± 0.7 (4)	Unknown	3.8± 0.4(3)	4.2 ± 0.3 (15)	5.0 (1)
Foot breadth	Unk.	Unk.	10.8 ± 1.6(3)	11.7 ± 1 (4)	Unknown	12.6±0.3(3)	13.4 ± 1.3 (15)	13.7±0.4(2)
Hand breadth	Unk.	Unk.	10.9 ± 1.8(3)	10.2±0.8(4)	Unknown	11.3±0.5(3)	11.7 ± 0.9 (16)	11.3± 0.1(3)
Thigh circum.	Unk.	Unk.	55 ± 6 (3)	62 ± 4 (4)	Unknown	75 ± 5 (3)	83 ± 7 (16)	89 ±11 (3)
Calf circum.	Unk.	Unk.	38 ± 6 (3)	43 ± 3 (4)	Unknown	47 ± 4 (3)	51 ± 3 (16)	56 ± 8 (3)

Table V. 5B. ***Continued***

	Infant (Ia) (0-1½ mo)	Infant (Ib) (1½-3 mo)	Infant (Ic) (4½-5¾ mo)	Infant (Id) (5¾-7¼ mo)	Infant (Ie) (7¼-9¾ mo)	Young Adult	Adult	Old Adult
Arm circum.	Unk.	Unk.	44 ± 7 (3)	42 ± 1 (4)	Unknown	51 ± 6 (3)	54 ± 5 (16)	56 ± 2 (3)
Forearm circum.	Unk.	Unk.	46 ± 8 (3)	36 ± 4 (4)	Unknown	42 ± 4 (3)	42 ± 3 (16)	45 ± 8 (3)
Chest circum.	Unk.	Unk.	102 ± 25 (3)	117 ± 9 (4)	Unknown	124 ± 5 (3)	136 ± 9 (17)	144 ± 16 (2)
Waist circum.	Unk.	Unk.	73 ± 13 (3)	95 ± 9 (4)	Unknown	106± 10(3)	109 ± 21 (16)	112 ± 10 (3)
Testicle (mm^3)	Unk.	Unk.	56.1±56.2(3)	67.1±19.5(4)	Unknown	197± 53(3)	919 ± 271 (17)	687±212(3)
Gland area (mm^2)	Unk.	Unk.	3.7 ± 6.4 (3)	12.3±24.7(4)	Unknown	0 ± 0 (3)	119 ± 77 (14)	101 ± 27 (3)

Table V. 5C: Mean values of each morphometric value across age-classes for female *Saguinus imperator*.

	Infant (Ia) (0-1½ mo)	Infant (Ib) (1½-3 mo)	Infant (Ic) (4½-5¾ mo)	Infant (Id) (5¾ -7¼ mo)	Infant (Ie) (7¼-9¾ mo)	Young Adult	Adult	Old Adult
Upper canine	Unknown	2.6 (1)	3.0 (1)	3.3 (1)	2.5 ± 0.9(3)	5.6 ± 1 (4)	6.1 ± 0.4 (8)	4.3 (1)
Lower canine	Unknown	1.7 (1)	1.7 (1)	2.2 (1)	2.4 ± 0.2(3)	5.1 ± 0.7 (4)	4.9 ± 0.4 (8)	3.7 (1)
Head	Unknown	36.3 (1)	40.3 (1)	41.9 (1)	45.2±0.4(2)	39.2 ± 12.5 (4)	43.8 ± 4.3 (8)	45.6 (1)
Tail	Unknown	287 (1)	321 (1)	315 (1)	329 ± 27(3)	357 ± 30 (3)	361 ± 15 (8)	380.5 (1)
Trunk	Unknown	122 (1)	150 (1)	160 (1)	167 ± 12 (3)	181 ± 19 (4)	199 ± 8 (8)	217.5 (1)
Total body	Unknown	445 (1)	511 (1)	517 (1)	560 ± 17 (2)	577 ± 27 (3)	603.8±20.6(8)	643.6 (1)
Upper leg	Unknown	49 (1)	57 (1)	65 (1)	66 ± 8 (2)	80 ± 5 (3)	78 ± 4 (8)	81 (1)
Lower leg	Unknown	54 (1)	65 (1)	68 (1)	70.3±2.5(2)	80 ± 2 (3)	79 ± 3 (8)	82 ± 4 (2)
Upper arm	Unknown	49 (1)	49 (1)	48 (1)	51.3± 1.8(2)	62 ± 7 (3)	63 ± 2 (8)	62 (1)
Forearm	Unknown	37 (1)	47 (1)	46 (1)	48.5±0.7(2)	58 ± 4 (3)	59 ± 3 (8)	57 (1)
Foot	Unknown	26.6 (1)	49 (1)	56.6 (1)	52.9±4.6(2)	56.2 ± 3.0 (3)	56.8 ± 3.6 (9)	60.4 (1)
Hand	Unknown	32.7 (1)	36.6 (1)	40.4 (1)	42.3±2.7(2)	47.0 ± 2.3 (3)	42.6 ± 2.2 (8)	44.1 (1)
Hand nail	Unknown	1.9 (1)	2.7 (1)	1.9 (1)	2.7 ± 0.4(2)	3.1 ± 0.4 (3)	2.7 ± 0.5 (8)	3.0 (1)
Foot nail	Unknown	1.3 (1)	2.8 (1)	2.3 (1)	3.1 ± 0.1 (2)	2.7 ± 0.4 (3)	2.9 ± 0.4 (8)	2.9 (1)
Foot breadth	Unknown	10.1 (1)	13 (1)	13.8 (1)	13.6±0.5(2)	14.5 ± 1.0 (3)	15.3 ± 0.6 (8)	15.7 (1)
Hand breadth	Unknown	12.5 (1)	12 (1)	13.4 (1)	14.1± 0.5(2)	14.7 ± 1.2 (3)	14.8 ± 0.8 (8)	15.4 (1)
Thigh circum.	Unknown	42 (1)	55 (1)	71 (1)	70.3±3.9(2)	91 ± 12 (3)	85 ± 6 (8)	94 (1)

Table V. 5C. *Continued*

	Infant (Ia) (0-1½ mo)	Infant (Ib) (1½-3 mo)	Infant (Ic) (4½-5¾ mo)	Infant (Id) (5¾-7¼ mo)	Infant (Ie) (7¼-9¾ mo)	Young Adult	Adult	Old Adult
Calf circum.	Unknown	39 (1)	42 (1)	42 (1)	49 ± 4 (2)	58 ± 5 (3)	56 ± 4 (8)	58 (1)
Arm circum.	Unknown	37 (1)	44 (1)	48 (1)	46.3±4.6(2)	63 ± 12 (3)	60 ± 5 (8)	65 (1)
Forearm circum.	Unknown	55 (1)	42 (1)	42 (1)	43.2±5.2(2)	54 ± 6 (3)	53 ± 4 (8)	58 (1)
Chest circum.	Unknown	93 (1)	97 (1)	113 (1)	116 ± 4 (3)	148 ± 11 (4)	146.8 ± 9.2 (8)	156 (1)
Waist circum.	Unknown	70 (1)	79 (1)	80 (1)	87 ± 4 (3)	89 ± 55 (4)	117.2 ± 13.9 (8)	121 (1)
Vulvar index	Unknown	12.4 (1)	13.3 (1)	16.6 (1)	14.0±1.6(3)	23.9 ± 7 (4)	22.3 ± 5.4 (8)	32.2 (1)
Nipple	Unknown	0 (1)	0 (1)	0 (1)	0 ± 0 (2)	3.0 ± 3.7 (4)	2.2 ± 2.4 (8)	5.0 (1)
Gland area (mm^2)	Unknown	0 (1)	0 (1)	0 (1)	0 ± 0 (3)	174.9±124.6(4)	138.6±104.9(8)	299.3 (1)

Table V. 5D: Mean values of each morphometric value across age-classes for male *Saguinus imperator*.

	Infant (Ia) (0-1½ mo)	**Infant (Ib) (1½-3 mo)**	**Infant (Ic) (4½-5¾ mo)**	**Infant (Id) (5¾-7¼ mo)**	**Infant (Ie) (7¼-9¾ mo)**	**Young Adult**	**Adult**	**Old Adult**
Upper canine	Unknown	Unknown	Unknown	Unknown	3.1 ± 0.2(3)	6.0 ± 0.9 (2)	6.0 ± 0.7(9)	5.0 ± 0.5 (3)
Lower canine	Unknown	Unknown	Unknown	Unknown	2.3 ± 0.1(3)	4.6 ± 0.1 (2)	4.8 ± 0.3(9)	4.6 ± 0.2 (3)
Head	31.4 (1)	Unknown	Unknown	Unknown	39.1±3.4(3)	45.1 ± 4.4 (2)	44.3±3.3(9)	46.2 ± 1.7 (3)
Tail	229 (1)	Unknown	Unknown	Unknown	326 ± 13(3)	360 ± 6 (2)	349 ± 10 (9)	361 ± 2 (3)
Trunk	124 (1)	Unknown	Unknown	Unknown	145 ± 0 (3)	183 ± 4 (2)	187.6±10.4(8)	194.8±9.0(3)
Total body	384 (1)	Unknown	Unknown	Unknown	510 ± 12 (3)	588 ± 15 (2)	580 ±15 (8)	602 ± 9 (3)
Upper leg	46 (1)	Unknown	Unknown	Unknown	62 ± 1 (3)	74 ± 2 (2)	76 ± 4 (9)	76 ± 4 (3)
Lower leg	50 (1)	Unknown	Unknown	Unknown	64 ± 1 (3)	78 ± 3 (2)	76 ± 4 (9)	78 ± 2 (3)
Upper arm	37 (1)	Unknown	Unknown	Unknown	52 ± 4 (3)	62 ± 2 (2)	60 ± 4 (9)	59 ± 3 (3)
Forearm	33 (1)	Unknown	Unknown	Unknown	45 ± 2 (3)	58 ± 1 (2)	55 ± 3 (9)	54 ± 2 (3)
Foot	39.6 (1)	Unknown	Unknown	Unknown	54.3±1.5(3)	57.2 ± 3.1 (2)	57.0±2.4(9)	56.1 ± 1.1 (3)
Hand	32.3 (1)	Unknown	Unknown	Unknown	41.8±0.5(3)	43.0 ± 0 (2)	43.4 ± 3 (9)	42.1 ± 2.7 (3)
Hand nail	2.4 (1)	Unknown	Unknown	Unknown	2.8 ± 0.2(3)	2.8 ± 0.1 (2)	2.9 ± 0.2(9)	2.9 ± 0.2 (3)
Foot nail	2.7 (1)	Unknown	Unknown	Unknown	2.5 ± 0.5(3)	2.8 ± 0.2 (2)	2.8 ± 0.4(9)	2.7 ± 0.6 (3)
Foot breadth	12.1 (1)	Unknown	Unknown	Unknown	13.4±0.4(3)	14.2 ± 4.2 (2)	14.7 ± 1.7(9)	15.5 ± 0.5 (3)
Hand breadth	11.9 (1)	Unknown	Unknown	Unknown	13.3±0.4(3)	14.6 ± 0.7 (2)	14.7± 1.2(9)	14.0 ± 0.3 (3)
Thigh circum.	46 (1)	Unknown	Unknown	Unknown	68 ± 2 (3)	94 ± 7 (2)	89 ± 8 (9)	88 ± 6 (3)
Calf circum.	36 (1)	Unknown	Unknown	Unknown	46 ± 3 (3)	54 ± 2 (2)	57 ± 5 (9)	56 ± 5 (3)
Arm circum.	34 (1)	Unknown	Unknown	Unknown	46 ± 2 (3)	63 ± 9 (2)	62 ± 2 (9)	58 ± 4 (3)
Forearm circum.	33.5 (1)	Unknown	Unknown	Unknown	44 ± 2 (3)	58 ± 7 (2)	55 ± 2 (9)	54 ± 6 (3)

Table V. 5D. ***Continued***

	Infant (Ia) (0-1½ mo)	Infant (Ib) (1½-3 mo)	Infant (Ic) (4½-5¾ mo)	Infant (Id) (5¾-7¼ mo)	Infant (Ie) (7¼-9¾ mo)	Young Adult	Adult	Old Adult
Chest circum.	82 (1)	Unknown	Unknown	Unknown	114 ± 3 (3)	154 ± 13 (2)	141 ± 11 (9)	137 ± 13 (3)
Waist circum.	60 (1)	Unknown	Unknown	Unknown	87 ± 7 (3)	114 ± 3 (2)	100 ± 8 (9)	98 ± 10 (3)
Testicle vol. (mm^3)	56.2 (1)	Unknown	Unknown	Unknown	126.9±44.3(3)	754.9±368.7(2)	800.0±233.7(9)	687.7±154.8(3)
Gland area (mm^2)	0 (1)	Unknown	Unknown	Unknown	0 ± 0 (3)	148.9 (1)	102.2 ± 64.6 (6)	41.4±71.7(3)

Table V. 5E: Mean values of each morphometric value across age-classes for *Saguinus fuscicollis* with sexes pooled.

	Infant (Ia) (0-1½ mo)	Infant (Ib) (1½-3 mo)	Infant (Ic) (4½-5¾ mo)	Infant (Id) (5¾-7¼ mo)	Infant (Ie) (7¼-9¾ mo)	Young Adult	Adult	Old Adult
Upper canine	Unknown	1.8 ± 0.4(3)	2.3 ± 0.6(5)	2.0 ± 0.2(7)	2.3 ± 0.2(6)	2.7 ± 3.8 (2)	5.1 ± 0.4 (40)	4.7 ± 0.7(6)
Lower canine	Unknown	1.7 ± 0.3(3)	2.1 ± 0.4(5)	1.9 ± 0.2 (7)	2.0± 0.3(6)	3.3 ± 1.6 (2)	4.4 ± 0.8 (40)	4.3 ± 0.3(6)
Head	Unknown	40.9 ± 8(3)	37.1± 3.6(5)	36.2±2.8(7)	38.7±2.0(6)	42.2 ± 2.0 (4)	43.5 ± 6.1 (37)	42.1±5.0(5)
Tail	Unknown	233 ± 3 (3)	266 ± 7 (5)	280 ± 13(7)	286 ±16 (6)	307 ± 17 (4)	316.3±16.2(38)	321 ± 28(6)
Trunk	Unknown	114 ± 5 (3)	136 ± 19 (5)	155 ± 9 (7)	161 ± 12 (6)	165 ± 15 (4)	183 ± 16 (38)	188 ± 11 (5)
Total body	Unknown	388 ± 8 (3)	439±24.6(5)	472 ± 21 (7)	486 ± 24(6)	514 ± 34 (4)	544 ± 27(36)	545 ± 40(6)
Upper leg	Unknown	48 ± 7 (3)	57 ± 5 (5)	63 ± 4 (6)	63 ± 4 (6)	71 ± 3 (4)	77 ± 5 (37)	79 ± 8 (6)
Lower leg	Unknown	54 ± 4 (3)	59 ± 4 (5)	69 ± 6 (6)	69 ± 4 (6)	74 ± 8 (4)	77 ± 5 (38)	80 ± 6 (6)
Upper arm	Unknown	39 ± 3 (3)	45 ± 5 (5)	52 ± 6 (6)	51 ± 3 (6)	57 ± 7 (4)	61 ± 4 (37)	63 ± 3 (6)
Forearm	Unknown	36 ± 5 (3)	46 ± 6 (5)	50 ± 6 (6)	49 ± 2 (6)	54 ± 7 (4)	58 ± 3 (37)	60 ± 4 (6)
Foot	Unknown	47.2±3.1(3)	50.7±7.0 (5)	50.1±2.7(6)	51.8±2.9(6)	53.1 ± 1.9 (4)	55.8± 3.0 (38)	54.0±3.4(6)
Hand	Unknown	32.6±1.8(3)	33.3± 2.6(5)	35.4±2.4(6)	35.5±2.0(6)	38.4 ± 2.2 (4)	40.5 ± 2.5 (38)	42.5±0.9(6)
Hand nail	Unknown	3.0± 0.4(3)	4.1 ± 0.5 (5)	3.8 ± 0.5(6)	3.9 ± 0.7(6)	3.7 ± 1.0 (4)	4.0 ± 0.5 (34)	4.2 ± 0.5(6)
Foot nail	Unknown	3.0 ± 0.1(3)	4.1 ± 0.4 (5)	3.8 ± 0.6(6)	4.1 ± 0.6(6)	4.1 ± 0.7 (4)	4.2 ± 0.5 (35)	4.9 ± 0.7(4)
Foot breadth	Unknown	10.7± 1.1(3)	11.7 ± 1.7 (5)	12.2± 1.2(6)	12.0±0.8(6)	13.0 ± 0.9 (4)	13.2 ± 1.7 (37)	13.9±0.5(5)

Table 5E. ***Continued***

	Infant (Ia) (0-1½ mo)	Infant (Ib) (1½-3 mo)	Infant (Ic) (4½-5¾ mo)	Infant (Id) (5¾-7¼ mo)	Infant (Ie) (7¼-9¾ mo)	Young Adult	Adult	Old Adult
Hand breadth	Unknown	9.8± 0.6(3)	11.4± 1.4(5)	10.1±0.9(6)	11.5± 1.6(6)	12.2 ± 1.7 (4)	11.4 ± 1.1 (38)	11.7±0.7(6)
Thigh circum.	Unknown	49.7±6.7(3)	64 ± 8 (5)	66 ± 9 (6)	70 ± 5 (6)	80 ± 11 (4)	82 ± 6 (38)	86 ± 9 (6)
Calf circum.	Unknown	34.3±2.5(3)	40 ± 5 (5)	44 ± 3 (6)	43 ± 4 (6)	49 ± 5 (4)	50.1 ± 4.0 (38)	53 ± 6 (6)
Arm circum.	Unknown	35.5±1.5(3)	42 ± 4 (5)	45 ± 6 (6)	44 ± 2 (6)	54 ± 8 (4)	54.2 ± 4.3 (37)	54 ± 3 (6)
Forearm circum.	Unknown	30.8±4.3(3)	33 ± 5 (5)	39 ± 6 (6)	38 ± 3 (6)	45 ± 6 (4)	42.2 ± 3.8 (37)	44 ± 5(6)
Chest circum.	Unknown	99 ± 8 (3)	106 ± 19(5)	121 ± 10 (7)	113± 13(6)	128 ± 10 (4)	137 ± 10 (38)	141 ± 13(5)
Waist circum.	Unknown	70 ± 5 (3)	82 ± 16 (5)	105 ± 23(7)	88 ± 17(6)	107 ± 8 (4)	109 ± 21 (38)	111 ± 11(6)
Testicle vol. (mm^3)	Unknown	Unknown	56.1±56.2(3)	67.1±19.5(4)	Unknown	197.0±52.6(3)	919.4±271.1(17)	686.5±211(3)
Nipple	0 (2)	0 (3)	0 (2)	0 (3)	0 (5)	0 (1)	1.5 ± 2 (21)	4.2 ± 0.3 (2)
Vulva Index	Unknown	9.1 ± 0.2(3)	12.2 ± 0.1(2)	10.3± 2.5(3)	10.7±1.4(6)	28.1 (1)	19.8 ± 3.9 (22)	24.5 ± 2.4(3)
Gland area (mm^2)	Unknown	0 (2)	2.2 ± 4.9 (5)	40.7 ± 42(7)	29.3±26.3 (6)	120.9±241.8 (4)	207.0±143.3 (36)	221.6±131.6 (5)

Table V. 5F: Mean values of each morphometric value across age-classes for *Saguinus imperator* with sexes pooled

	Infant (Ia) (0-1½ mo)	Infant (Ib) (1½-3 mo)	Infant (Ic) (4½-5¾ mo)	Infant (Id) (5¾-7¼ mo)	Infant (Ie) (7¼-9¾ mo)	Young Adult	Adult	Old Adult
Upper canine	Unknown	2.6 (1)	3 (1)	3.3 (1)	2.8 ± 0.6(6)	5.7 ± 0.9 (6)	6.1 ± 0.6(17)	4.8 ± 0.5(4)
Lower canine	Unknown	1.7 (1)	1.7 (1)	2.2 (1)	2.3 ± 0.2 (6)	4.9 ± 0.6 (6)	4.9± 0.3(17)	4.4 ± 0.5(4)
Head	31.4 (1)	36.3 (1)	40.3 (1)	41.9 (1)	41.6 ± 4.1(5)	41.2 ± 10.4 (6)	44.1±3.7(17)	46.0±1.4(4)
Tail	229 (1)	287 (1)	321 (1)	315 (1)	327 ± 19 (6)	358 ± 22 (5)	355 ± 13(17)	366 ± 10 (4)
Trunk	124 (1)	122 (1)	150 (1)	160 (1)	156 ± 14 (6)	182 ± 14 (6)	193 ± 11 (16)	201 ± 14 (4)
Total body	384 (1)	445 (1)	511 (1)	517 (1)	530 ± 30 (5)	581 ± 21 (5)	592 ± 21(16)	612 ± 22 (4)
Upper leg	46 (1)	49 (1)	57 (1)	64.5 (1)	63 ± 4 (5)	77 ± 5 (5)	77 ± 4 (17)	78 ± 4 (4)
Lower leg	50 (1)	54 (1)	65 (1)	68 (1)	66 ± 4 (5)	79 ± 2 (5)	77 ± 4 (17)	80 ± 3 (5)
Upper arm	37 (1)	49 (1)	49 (1)	48 (1)	52 ± 3 (5)	62 ± 5 (5)	61 ± 3 (17)	60 ± 3 (4)
Forearm	33 (1)	37 (1)	47 (1)	46 (1)	47 ± 2 (5)	58 ± 3 (5)	57 ± 4 (17)	54 ± 2 (4)
Foot	39.6 (1)	26.6 (1)	49 (1)	56.6 (1)	53.7± 2.7(5)	56.6 ± 2.7 (5)	56.9±2.9(18)	57.2± 2.3(4)
Hand	32.3 (1)	32.7 (1)	36.6 (1)	40.4 (1)	42 ± 1.4 (5)	45.4 ± 2.8 (5)	43.0±2.7(17)	42.6±2.4(4)
Hand nail	2.4 (1)	1.9 (1)	2.7 (1)	1.9 (1)	2.8 ± 0.3 (5)	3.0 ± 0.4 (5)	2.8 ± 0.4(17)	2.9 ± 0.1 (5)
Foot nail	2.7 (1)	1.3 (1)	2.8 (1)	2.3 (1)	2.7 ± 0.5 (5)	2.7 ± 0.3 (5)	2.9 ± 0.4(17)	2.8 ± 0.5(4)
Foot breadth	12.1 (1)	10.1 (1)	13 (1)	13.8 (1)	13.5± 0.4(5)	14.4 ± 2.2 (5)	15 ± 1.3 (17)	15.6± 0.4(4)

Table V. 5F. *Continued*

	Infant (Ia) (0-1½ mo)	Infant (Ib) (1½-3 mo)	Infant (Ic) (4½-5¾ mo)	Infant (Id) (5¾-7¼ mo)	Infant (Ie) (7¼-9¾ mo)	Young Adult	Adult	Old Adult
Hand breadth	11.9 (1)	12.5 (1)	12 (1)	13.4 (1)	13.6± 0.6(5)	14.6 ± 0.9 (5)	14.8 ± 1.0 (17)	14.4 ± 0.7 (4)
Thigh circum.	46 (1)	42 (1)	55 (1)	71 (1)	69 ± 3 (5)	92 ± 9 (5)	87 ± 7 (17)	89 ± 6 (4)
Calf circum.	36 (1)	39 (1)	42 (1)	42 (1)	48 ± 3 (5)	56 ± 4 (5)	56 ± 4 (17)	57 ± 4 (4)
Arm circum.	34 (1)	37 (1)	44 (1)	48 (1)	46 ± 3 (5)	63 ± 9 (5)	61 ± 4 (17)	60 ± 5 (4)
Forearm circum.	34 (1)	55 (1)	42 (1)	42 (1)	44 ± 3 (5)	55 ± 6 (5)	54 ± 3 (17)	55 ± 5 (6)
Chest circum.	82 (1)	93 (1)	97 (1)	113 (1)	115 ± 3 (6)	150 ± 11 (6)	144 ± 11 (17)	142 ± 14 (4)
Waist circum.	60 (1)	70 (1)	79 (1)	80 (1)	87 ± 5 (6)	97 ± 45 (6)	108 ± 14(17)	104 ± 14(4)
Nipple	Unknown	0 (1)	0 (1)	0 (1)	0 (2)	3.0 ± 3.7 (4)	2.2 ± 2.4(8)	5.0 (1)
Vulva Index	Unknown	12.4 (1)	13.3 (1)	16.6 (1)	14.0±1.6(3)	23.9 ± 7.0 (4)	22.3±5.4(8)	32.2 (1)
Testicle vol. (mm^3)	56.2 (1)	Unknown	Unknown	Unknown	126.9 (3)	754.9±368.6(2)	800±233.7(9)	688±155(3)
Gland area (mm^2)	0 (1)	0 (1)	0 (1)	Unknown	0 (6)	169.7±108.6(5)	123.0±88.7(14)	106±142(4)

Table V. 6: Percent of mean adult values for morphometric variables in both species, at different ages, for which known-age individuals exist.

	Saguinus fuscicollis			***Saguinus imperator***		
	3 mo	6 mo	17 mo	3 mo	6 mo	16-19 mo
Upper canine	36	40	100	45	49	90
Lower canine	38	43	92	35	48	99
Head	82	82	93	42	76	100
Tail	73	88	100	72	91	99
Trunk	61	82	94	63	80	95
Total body	71	87	98	70	89	100
Upper leg	63	81	100	61	82	100
Lower leg	69	88	99	66	85	98
Upper arm	63	84	98	70	83	100
Forearm	61	86	97	62	83	100
Foot	85	90	100	58	95	100
Hand	80	87	100	76	97	100
Hand nail	73	92	97	77	94	100
Foot nail	70	90	96	69	92	100
Foot breadth	81	92	96	74	90	95
Hand breadth	86	89	100	83	92	90
Thigh circum.	60	80	100	50	79	86
Calf circum.	67	86	95	67	83	93
Arm circum.	66	84	99	58	76	86
Forearm circum.	60	77	81	82	81	86
Chest circum.	72	88	93	61	80	94
Waist circum.	65	88	90?	61	80	100
Nipple	0	0	0	0	0	0
Vulva Index	45	51	84	53	63	56
Testicle vl. (mm^3)	Unk.	8	100	7	16	Unk.
Male gland area (mm^2)	Unk.	11	64	0	0	Unk.
Female gland area (mm^2)	0	29	53	0	0	0

SF = *Saguinus fuscicollis*; SI = *Saguinus imperator*; Unk. = Unknown;

The last column compares the two species with sexes pooled.

V. 3. 3: Scent-glands and Genitalia

The scent glands and genitalia differ markedly in appearance by sex and species, making confident sex assignations possible based on appearance alone (Fig. V. 2 and V. 3). However, at a very young age, they are not distinguishable and the keys provided in this study are based on sex identifications confirmed at an older age.

V. 3. 3. 1: Scent Gland and Genitalia Morphology and Sizes

Mean vulvar indices of older adult females are not significantly different than those of adult females in either *S. fuscicollis* or *S. imperator* (Mann-Whitney *U: P* ≥ 0.05). Mean adult values were calculated for both age classes pooled, and are not significantly different between the two species. Testicular volume in males displayed similar trends, and does not differ between adult and older adults in either species, or between the species themselves. In *S. fuscicollis*, vulvar indices are at *ca*. 50% of adult values at 6 mo of age, and by 17 mo, achieve *ca*. 84% of mean adult values (Table V. 6). However, we see vulvar indices holding steady at 50 to 60 % of adult values between 3 and 19 mo of age with *S. imperator*, indicating later development of vulvas as compared to *S. fuscicollis* (Fig. V. 5C). Data for testicular volumes are missing for the 3 mo mark in *S. fuscicollis*, and the 16-19 mo mark in *S. imperator*, due to individuals of those known ages being females. Nevertheless, as compared to vulvar indices, testicular volumes reach only 8% of their adult value for *S. fuscicollis* and 16% of adult values for *S. imperator* at 6 mo of age. Between 6 and 17 mo, we know that male *S. fuscicollis* achieve full adult values as well, showing an initial delay in testicular growth in males compared to vulvar growth in females (Fig. V. 5D). However, by 1.5 yr of age, males appear to have testicular morphology of adults, while females in both species do not display adult vulvar morphology. Male captive cotton top tamarins display a spurt of dihydrotestosterone at 40-44 weeks of age (*ca*. 11 months), which could explain delayed development early on followed by subsequent rapid testicular development.

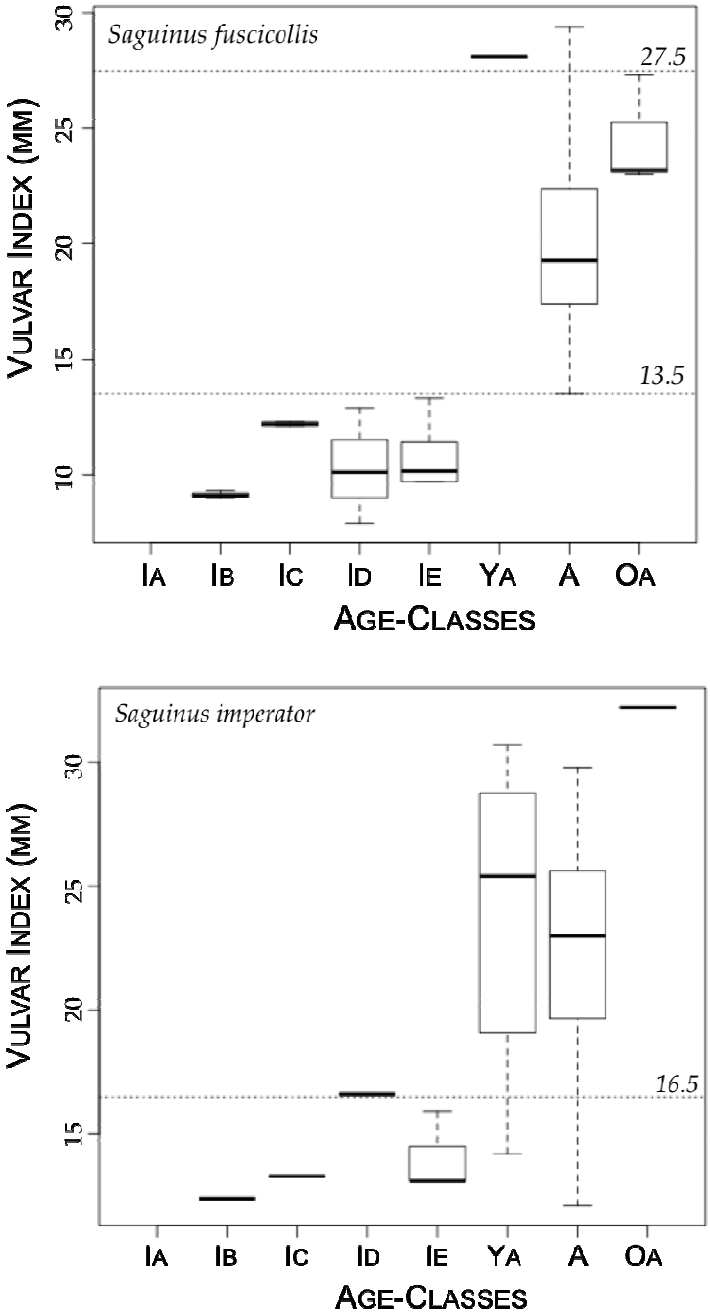


Figure V. 5C: Vulvar index distribution across the age-classes for both species. Infant age-classes are subdivided further as follows: I_A (0-1½ mo), I_B (1½-3 mo), I_C (4½-5¾ mo), I_D (5¾-7¼ mo), I_E (7¼-9¾ mo). Adult classes include YA (young adults), A (adults), and OA (old adults). Visible cut-offs are marked with a dotted line.

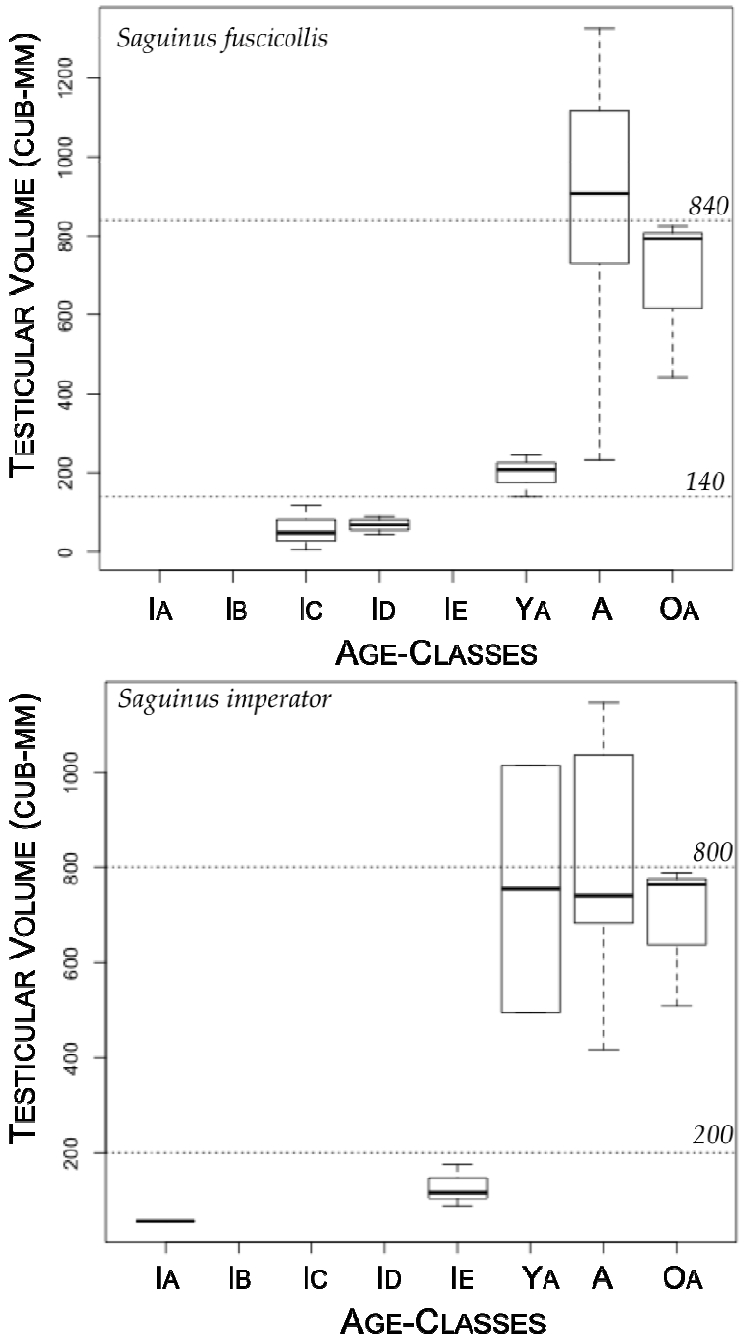


Figure V. 5D: Testicular volume distribution across the age-classes for both species. Infant age-classes are subdivided further as follows: I_A (0-1½ mo), I_B (1½-3 mo), I_C (4½-5¾ mo), I_D (5¾-7¼ mo), I_E (7¼-9¾ mo). Adult classes include YA (young adults), A (adults), and OA (old adults). Visible cut-offs are marked with a dotted line.suprapubic gland area (calculated as the product of length and breadth).

Suprapubic gland morphology is highly variable within and between the two species, with larger more visible glands in females rather than males overall. This difference is particularly exaggerated between the two sexes in *S. fuscicollis*, where it is significantly higher in females than males ($P \leq 0.05$) (Table V. 3). Gland areas are not significantly different between adult and older adult age classes in either species, and so adult values are calculated from the pooled means of these two age classes. At 6 mo of age, male *S. fuscicollis* are well behind their female counterparts in terms of percent adult values for gland area achieved; however, by 1.5 yr, males (64%) have surpassed females (53%) in suprapubic glandular development, but neither has achieved full adult values (Table V. 6). *Saguinus imperator* shows no development at all of suprapubic glands up to at least 1.5 yr in females and 6 mo in males (no males of 1.5 yr were observed). Glands in *Saguinus imperator* were not highly pigmented as with *S. fuscicollis*, making them only visible as raised portions of slightly accentuated skin above the vulva or scrotum (Fig. V. 2). We also find high variability in adult values of gland area in males and females of both species, implying the possible involvement of factors other than age in determining development of this feature (Table V. 3).

Generalised linear models were developed to determine if suprapubic gland areas were correlated with genitalia dimensions, while controlling for individual weight. Linear regressions indicate that vulvar indices explain *ca.* 70% of variation in suprapubic gland area for females of both *S. fuscicollis* ($R^2 = 0.70$, $P \leq 0.001$) and *S. imperator* ($R^2 = 0.76$, $P \leq 0.001$). While a similar trend is observed with testicular volume and suprapubic gland areas in male *S. fuscicollis* ($R^2 = 0.63$, $P \leq 0.001$), we do not see the same with male *S. imperator*.

V. 3. 3. 2: Scent Gland and Genitalia Scores and Cutoffs

Spearman rank correlations revealed that vulvar and scrotal scores are significantly correlated to vulvar indices ($r_s = 0.85$, $P \leq 0.001$) and testicular volumes ($r_s = 0.56$, $P \leq 0.05$), respectively, in *Saguinus fuscicollis*. While female *S. imperator* have vulvar indices that are highly correlated to vulvar scores ($r_s = 0.80$, $P \leq 0.001$), testicular volumes in males of this species were not significantly correlated with scrotal scores. Female *S. fuscicollis* scores for vulva ($r_s = 0.68$, $P \leq 0.001$) are significantly correlated with age-class, as are scores for *S. imperator* ($r_s = 0.63$, $P \leq 0.001$).

The idea of using certain values for genitalia as cutoffs to determine adulthood was suggested by Soini (Soini & Cóppula 1981) (testicular volume 430 mm^3 and vulvar index of 19) and has been used by others as a reference (Garber et al. 1996). In this study, where age-classes were assigned based on dentition and not merely genitalia size in comparison to body mass, despite mean vulvar indices being > 19 mm in both species, we see that several adult individuals routinely have vulvar indices < 19 mm. All infants of *S. fuscicollis* had vulvar indices < 13.5 mm, while those of *S. imperator* had indices < 16.5 mm. While older adult *S. fuscicollis* had vulvar indices 27.5 mm and lower, which is slightly lower than adult and young adult values, those of *S. imperator* appear to have higher values than the other age-classes. Male infants of *S. fuscicollis* do not have testicular volumes exceeding 140 mm^3, while infants of *S. imperator* do not cross 200 mm^3. Adult testicular volumes in *S. fuscicollis* do not adhere to the cut off of 430 mm^3, but adult *S. imperator* do. Further, we do see that older adult males of both species remain below a cut off of 800 to 840 mm^3. It appears that the use of specific values of vulvar indices and testicular volumes can be used to tell infants from other age-classes, but adults cannot be distinguished from the other age-classes for either species.

V. 3. 4: Nipple Lengths and Parity

Soini (1981) indicated that a female with nipples > 3 mm is generally likely to have been pregnant currently or in the past, so nipple lengths were measured on all females where visible. We did not find a single female up to 1.5 yr of age in either species with nipple lengths > 3 mm. Out of 17 instances of recording nipple lengths in female *S. fuscicollis* in individuals up to the young adult age-classes, none appeared to have carried a pregnancy to term based on this standard (Table V. 5A). While 5 instances of measurement of nipple lengths in the infant classes of *S. imperator* showed no parous females, the four young adult females averaged a nipple length of 3 mm (Table V. 5C). Adult female *S. fuscicollis* displayed highly variable nipple lengths (1.4 ± SD 2.0 mm), many < 3 mm, indicating that several adult females had not reproduced even once (Table V. 5A). On the other hand, the three older adult female *S. fuscicollis* were observed to all have nipple lengths > 3 mm. A single older adult female was observed to have a nipple length of 5 mm.

V. 3. 5: Seasonal Differences

In order to avoid the effects of pseudoreplication, I used adjusted body weights in this analysis that have been averaged within age-classes to avoid individual effects. We found no significant differences between the body weights of individuals who have attained adult body mass (all except those of AC "Infant") across months (Kruskal-Wallis rank sum test, $p \geq 0.05$) for males or females of either species, with one exception. The body weights of female *S. imperator* appear to be affected significantly by month ($p \leq 0.05$, df = 2), and post hoc analyses reveal that they are heavier in April (mean 599 ± *SD* 34, N = 5) than they are in June (mean 448 ± *SD* 75, N = 4). The lack of this observed in *S. fuscicollis* is likely due to lower numbers sampled from this species in April.

Upon analyzing testicular volume, vulvar indices or suprapubic gland areas, no significant effect of month was found on any of these measures (Kruskal-Wallis rank sum test, $p \geq 0.05$). However, since the capture and release program is conducted only once each year, with the timing of capture dependent on feasibility, regular measurements in the wet and dry seasons are not feasible. As further years are added, clearer trends might be seen across months, but with the present dataset, we do not have evidence to suggest that seasonality affects these measures. Therefore, looking at the mean values across different months for each of these variables allows us to identify possible trends based on seasonality that can then direct future sampling efforts (Table V. 7).

Table V. 7: Monthly variation of reproductive measures and body mass for males and females of both species. All values are represented as Mean ± SD, numbers in parentheses indicate the number of samples.

	January	**March**	**April**	**May**	**June**	**July**	**November**	**December**
Weight of ♀ *S. fuscicollis* (g)	417 (1)	412±13(3)	400 ±24(4)	427±39(4)	381 ± 35(9)	391 ± 37 (5)		
Weight of ♂ *S. fuscicollis* (g)		420±14(2)		405±37(5)	347± 60(6)	360 ± 51 (6)	363± 39 (2)	339± 41 (2)
Weight of ♀ *S. imperator* (g)			599± 34 (5)	577±49(4)	448± 75(4)			
Weight of ♂ *S. imperator* (g)			504± 42 (7)	511±82(3)	488± 57(4)			
Testicular vol. *S. fuscicollis* (mm^3)		754±45(2)		897±163(5)	763±479(6)	802±370(6)	443 (1)	820±509(3)
Testicular vol. *S. imperator* (mm^3)			746±243(7)	831±160(3)	764±275(4)			
Vulvar index of *S. fuscicollis* (mm)	22.3 (1)	20.1±6.5(2)	20.5±2.1(4)	20.7±5.8(5)	19.9±4.8(9)	22.0±3.7(5)		
Vulvar Index of *S. imperator* (mm)			26.8±4.8(5)	24.4±1.9(4)	18.7±7.9(4)			
Gland Area ♂ *S. fuscicollis* (mm^2)		88 (1)		82 ± 20(4)	97 ±107(8)	114±76(6)		
Gland Area ♂ *S. imperator* (mm^2)			213±126(5)	188 ±48(4)	74 ±101(4)			
Gland Area ♀ *S. fuscicollis* (mm^2)	606 (1)	244±211(2)	289±164(4)	275±178(5)	240±138(9)	277±44(5)		
Gland Area ♀ *S. imperator* (mm^2)			71±101(2)	128±30(3)	72 ± 77(5)			

Note: Data was collected based on the feasibility of trapping, and not specifically to check for monthly changes in these measures. Therefore, several months are not represented in the data set. Data also include all individuals except those in the infant class.

V. 3. 6: Pelage Changes

Infant *Saguinus fuscicollis* are born covered in black hair, with no visible saddle or rust coloration of the hindquarters. They also have a distinctive facial coloration involving white cheek patches on either side of a flattened, dark colored snout. The V-shaped white hair on the brow, distinctive to the subspecies *S. f. weddelli*, begins as a diffuse patch of light colored fur in a dark face. Subsequently, as the infants age, the snout becomes prognathic and covered in white hair, the white cheek patches disappear, and the more exact V-shaped eyebrow is formed (Fig. V. 4A). Infants of *S. imperator* are quite similar to adults in the overall grey pelage of the body, but differ in facial coloration and development. When very young, they have extremely short whiskers and a flattened snout covered in white hair. As they grow, the snout becomes prognathic and pink, and they develop a luxurious set of mustaches accompanied by beard-like hairs on the chin (Fig. V. 4B).

We found a large amount of variation in facial pelage development in *S. fuscicollis*, with individuals up to 6 months of age still exhibiting significant cheek patches with dark colored and flattened snouts (Score 1) (Fig. V. 6). From 2.5 months to *ca.* 7 mo of age, they slowly transition from dark snouts to lighter snouts, with steadily reducing cheek patches and better-defined white V-shaped brows. By *ca.* 7 mo, all infants had prognathic snouts with minimal cheek patches (Scores 3 or 4). Finally, by 10 mo of age, all individuals have adult facial development and coloration (Fig. V. 6).

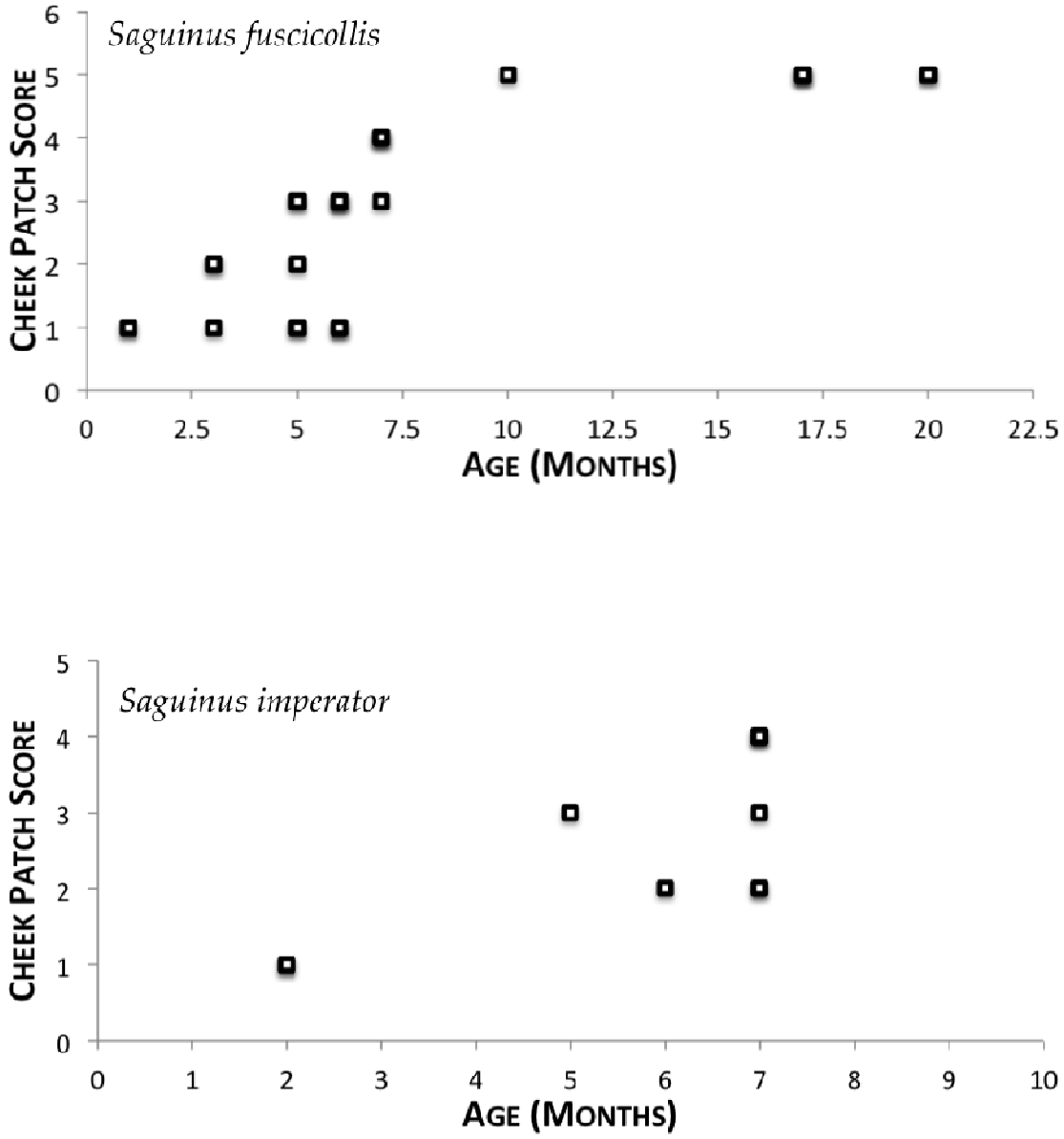


Figure V. 6: Cheek patch scores plotted against chronological age. Since an additional year of data is available for *S. fuscicollis*, scores up to 22½ months are included for this species.

With a slightly smaller dataset on *S. imperator*, we were still able to track facial development through infancy. At 2 mo of age, all individuals appear to have very little development from the classic infant model of no whiskers in a flattened snout (Score 1). However, between the ages of 5 and 6 mo, we see lots of variation in facial development with individuals exhibiting moderate facial development (Fig. V. 6). At 7 mo of age, we see the first individuals with fully adult pelage, and since we are lacking data on individuals older than 7 mo of age, we cannot be entirely sure when exactly all infants are sure to have adult facial coloration and development.

V. 4: Discussion

Our morphometric data on *Saguinus fuscicollis* and *S. imperator* have allowed us to look at morphological differences in reproductive and somatometric measures over age groups and, to a lesser extent, season. Few studies on wild primate populations have access to such information through capture and release programs, and fewer still have longitudinal data on these measures (Glander et al. 1992; Hamada et al. 2006; Jolly & Phillips-Conroy 2003; King et al. 2011; Soini & Cóppula 1981). Since this is a report on the first years of data collection at this site, we still have more individuals of unknown rather than known chronological ages. With further study this dataset should yield measures for known individuals over several years, which will allow us to compute growth curves across the lifespan of an individual.

V. 4. 1: Body Mass and Pregnancy

Estimates of age based on dentition allow us to identify likely birth months for each infant (Chapters IV and VI). Given a *ca.* 5 mo gestation period (140 days Hershkovitz 1977b), we examined known females who had given birth to find that *Saguinus fuscicollis* could be pregnant from early April to late January, while *S. imperator* could be pregnant from early June to early March. Thus far, we found that only a single female *S. fuscicollis* could be confirmed to be in her first month of pregnancy during capture. We did not capture animals in 2009, and in

2011, all captures occurred in April and May when animals could be in very early stages of pregnancy. In 2012, we could have assessed pregnant females in their 1st or 2nd month of pregnancy; however, it is difficult to exclude them without knowing if they are pregnant or carry pregnancies to term in 2013. Additionally, only a small number of females could likely be pregnant at all, of which fewer still are likely to be in advanced stages of pregnancy where weights could differ (Garber & Teaford 1986b). Therefore, we conclude that pregnancies in this dataset are unlikely to cause significant bias to mean body mass.

V. 4. 2: Species Differences in Body Mass and Measurements

Weights of adult *Saguinus imperator* indicate that they are significantly heavier than *S. fuscicollis*, and this pattern is upheld between the males and females of each species as well. Upon examining limb lengths as well as circumferences, we found that this increase in body mass is driven not by an overall increase in linear dimensions (i.e. body or limb lengths) in *S. imperator*, but instead, considerably thicker limbs. The acquisition of this additional weight by *S. imperator* is reflected in growth differences between the species as well; while, growth rates are higher before the age of 6 months than they are for animals 6 to 12 months of age in *S. fuscicollis*, we see a large growth spurt from 6 to 12 months of age in *S. imperator*. Further, limb circumferences increase at a slower rate than limb lengths in both species, and it is after circumferences achieve adult values that *S. imperator* achieves its higher overall body mass.

Several other measures appear to be different between the two species, generally indicating the overall robustness of *S. imperator* over *S. fuscicollis*. Canine, trunk, tail and total body lengths were all significantly higher in *S. imperator*, and interestingly, although *S. imperator* had wider hands and feet, they had significantly shorter nail lengths than *S. fuscicollis*. In appearance, *S. fuscicollis* has extremely long and curved nails, with very little actual wear on them, whereas the nails on *S. imperator* nails appear worn down and blunt. This could very likely be due to the additional weight that *S. imperator* carry, without an overall

increase in size. This could also relate to why *S. fuscicollis* frequently use large vertical substrates (Garber & Leigh 2001). These data encourage further study of the locomotor and substrate use differences between the two species.

V. 4. 3: Species Differences in Genitalia and Scent Glands

Genitalia and scent glands in the two species differ widely in appearance, with *S. fuscicollis* possessing more pigmented genitalia, as well as more visible scent glands. However, there are no significant differences between the species in testicular volumes or vulvar indices. Vulvas grow slower in *S. imperator* than in *S. fuscicollis*, based on rates of increase in vulvar indices, indicating the possibility that *S. fuscicollis* could engage in sexual activity earlier than *S. imperator*. Unfortunately, less data on testicular volumes of known individuals for both species are available than data on vulvar indices; nevertheless, we can be sure of a few trends. First, testicular volumes grow very slowly in males of both species, up to 6 months of age. For *S. fuscicollis* at *ca*. 1.5 yr of age, we show that full adult volumes have indeed been achieved, and this data set does not allow us to comment on *S. imperator* in this regard. Scent glands develop unequally in both species, with much faster development observed in *S. fuscicollis*. Furthermore, when vulvar indices are high, we find that there is a strong chance that suprapubic gland areas would be large in females of both species, after controlling for weight. While this trend is visible in testicular volumes and suprapubic gland areas of male *S. fuscicollis*, there appears to be no correlation between scent gland areas and testicular volumes in *S. imperator*.

We believe that this particular change in pattern for *S. imperator* could be explained by a few different factors. Firstly, *S. imperator* possesses another visible gland that they use to deposit scents, located over the sternum. This sternal gland, although present, is so small and covered with hair that it is hard to assess in terms of size or development. Secondly, it is possible that the external appearance of a gland does not directly relate to the internal structure or functionality of the gland as a whole (Hershkovitz 1977b), which could in turn explain the lack

of correlation between the slightly diffuse glands in male *S. imperator* and their testicular development.

Although we do not have scent-marking behavioral data analyzed at this time, this data set exists and the scent-marking behavior will be correlated to the morphology of the glands in a future publication. In general however, we observe that infants of both species do not participate in this behavior until at least 6 months of age, although this does not necessarily imply that they are not capable of producing olfactory secretions from the glands during this time; secretions from the glands of infant *C. jacchus* a mere two weeks after birth produces serum testosterone depression in males with experience in offspring-rearing (Prudom et al. 2008).

Young adult and adult *S. imperator* also display highly variable nipple lengths, with slightly lower mean values among adult females. These values imply that *S. imperator* likely requires a higher cutoff value (e.g. 4 mm) than *S. fuscicollis* to determine parity.

V. 4. 4: Sex Differences in Body Mass and Morphology

We found no sexual dimorphism of body mass in adults of either species. Growth over time, as reflected by increases in body mass, does not appear to be significantly different between the sexes, although females show a slight trend toward faster body mass growth than males. In fact, the only measurement found to be sexually dimorphic in both species was the upper arm length, which is longer in females than males, a difference that cannot be explained by measurement method differences or errors. Further, in *S. imperator* alone, waist circumferences are also larger in females than males. While this could be an early indication of pregnancy, there's no difference in body weights between the sexes, nor are these females expected to be pregnant at this time (See Chapter VI).

V. 4. 5: Sex Differences in Scent Gland and Genitalia Morphology

Females in both species have more visible suprapubic scent glands than the males, and it would be interesting to see if this corresponds to the frequency at which they deposit scents. In general, there appears to be a high amount of variability in the area of suprapubic glands across both sexes and species, which could imply that factors other than merely sex or species affect these values. Male *S. fuscicollis* appear to be delayed relative to females in terms of suprapubic gland development at 6 mo of age, but by 1.5 yrs of age, have overshot suprapubic gland growth in females; however, neither males nor females actually achieve full adult values for their suprapubic glands by 1.5 yr of age. On the other hand, male *S. imperator* develop their glands at 6 mo of age, while females do not achieve visible glands at even 1.5 yr of age. These inconsistencies in suprapubic gland development could have strong effects on scent marking behaviors (to be explored in future work) as well as sexual activity, if scent marking is tied to sexual maturity as it is thought to be (Caspers et al. 2011; Epple 1982; Heymann 2001; Lazaro-Perea et al. 1999). We also note that while genitalia achieve adult values in males by 1.5 yr of age (in *S. fuscicollis* only, for which we have this data), vulvas do not reach full adult values at this age in either species. Again, this is possibly reflected in different rates of initiation of sexual activity in males and females of both species.

V. 4. 6: Scoring Systems

The scoring systems described in this chapter we believe are valuable to field biologists as a system to evaluate the sexual maturity, age and development of individuals of these species in the wild. Capture and release programs utilize an anesthetic to sedate animals, and in general, it is advisable to reduce the amount of time an animal spends unconscious. This often puts a great deal of strain on the handler, and in such situations, if detailed measurements are not feasible, genitalia and scent glands can reliably be scored from a simple photograph. We found the scoring system presented here to be consistent in evaluating infants from other age classes

(but not young adults from adults) except in the case of the scrota of *S. imperator*, in which coloration differences are subtle unlike with *S. fuscicollis*.

Although a system of using specific cutoff values to determine adulthood and sexual maturity in *S. fuscicollis* has been outlined in the past (Soini & Cóppula 1981), sufficient evidence to support the continued use of these values and this system was not available in this population. It is quite possible that the larger sample size, wild conditions, or differing measurement techniques can explain this finding. Further, Soini (1981) could also have implied that the cutoffs were a general value that all individuals might not consistently uphold, but that were appropriate to use in most cases. Interestingly, we found that the infant age class often had distinctive enough values for most reproductive measures that it could be consistently said to be below a certain value, but it is certainly impossible to do the same with adults in this population.

V. 4. 7: Seasonality

This study used data collected during capture and release efforts, the timing of which was determined largely by the feeding ecology and the availability of resources to the callitrichid species in question. Animals were regularly censused over at least 5 months each year, but captured only once typically between the months of April and July. These months fall squarely within the dry season, with limited fruit availability that encourages them to enter traps and consume bait placed there. Therefore, testing for seasonal differences or the effect of capture month on variables such as body mass and reproductive measures is difficult, and encourages further sampling across the wet season. No significant effect of month was found on body mass, testicular volumes or vulvar indices in either species, with one exception – female *S. imperator* were heavier in wet April than they were in dry July, which implies that the dry season does indeed affect weights cyclically through the year. We see slight trends towards this pattern in the remaining measures, but none show significant differences, even in the case of a few *S.*

fuscicollis that were captured in the wet season of 2009. This supports the further sampling of these individuals in the wet season if possible, which might now be possible, finally, as animals are increasingly habituated to the bait and might descend to eat the fruit despite other options for food available naturally. Finally, we see smaller standard deviations, implying less variability in gland areas, in the month of July over April, May and June, which coincides with the close of intensive mating as most females would likely be pregnant by this time. It is possible that those with larger gland areas might be more sexually active as well, and gland areas therefore affect breeding status in groups (see Chapter VI).

V. 4. 8: Inferences for Breeding Status

The distribution of morphometric measures across age-classes through cross-sectional data on a species is the first step toward building a model of growth and development across a lifespan (King et al. 2011). There is additional significance to cross-sectional or minimally longitudinal data on reproductive measures across known individuals in a population. First, these measures can be used in a broad sense to compare sympatric species, as we have in this chapter, to deem if there exist significant overlaps in the range of variation of certain traits in two species (Hamada et al. 2005). It can also inform the categorization of the reproductive status of an individual, for e.g. into primary or secondary breeding positions, when considered in conjunction with observed reproductive and parenting behaviors (see Chapter VI). This could be in the form of identifying specific thresholds that delineate breeding categories (e.g. Soini & Cóppula 1981), or in identifying markers that delineate parity in females, or sexual maturity in either sex. Moreover, these measures can inform our ideas of when and why an animal disperses to a new group, and whether that choice is driven by its morphological development or if its development changes in response to the act of dispersal itself (see Chapter VII).

It is important to note that age-classes, especially adults and younger adults, cannot be differentiated based on the sizes of genitalia and suprapubic glands in this species. This further

confirms that error could be introduced by defining age based on reproductive measures alone, and that dentition is a more accurate marker for age among callitrichids. This is most likely due to possible reproductive suppression of secondary breeders or nonbreeders by primary breeding individuals, and both males and females are known to exhibit suppression in other callitrichid species (Baker et al. 1999; Epple & Katz 1984).

V. 5: Chapter Summary

1. Adult *Saguinus imperator* are significantly heavier than adult *S. fuscicollis*, as are the individual sexes across species, but no sexual dimorphism was observed for other somatometric measurements. This increased weight of *S. imperator* derives from increased limb circumferences and not limb lengths.
2. Although the genitalia differ in appearance between species, there are no significant size differences observed.
3. Suprapubic glands also differ in appearance between the sexes, and we see significantly higher glandular areas among females than males, with the extent of this difference being greater in *Saguinus fuscicollis* than in *S. imperator*.
4. Suprapubic gland areas and genitalia sizes are correlated for all groups, except for male *Saguinus imperator* whose glands are subtle and often hard to measure.
5. Morphological scores assigned to genitalia and glands encompass their variability, and are good proxies for distinguishing infants from adult class, but not other age classes. The single exception again is with male *Saguinus imperator*.
6. Although cutoffs for gland and genitalia sizes have been suggested in the past, we found that this population's measurements did not conform to the cutoffs suggested to determine age in most cases, and we attempt to revise these values for these species. However, in general, it does not appear that all age-classes can be distinguished very well based solely on genitalia sizes.

7. This last point highlights the singular importance of judging age based on dental categories and not on reproductive measures, since these could be affected by possible reproductive suppression in this species.

Chapter VI. Inferring Reproductive Status of Sympatric Callitrichidae from Morphology and Age

VI. 1: Introduction

Increasingly, studies of callitrichids reveal more flexible behavior and population structures than previously expected; however, this is accomplished without reducing the stability of individual groups (Goldizen et al. 1996; Löttker et al. 2004a; Terborgh & Goldizen 1985). In the early days of research on callitrichid biology, a certain archetype of the cooperatively breeding primate emerged in the literature. Each group was hypothesized to contain a habitually twinning (Hampton & Hampton 1965b), polyandrous, dominant female that, driven by the high energetic costs to raising twins (Tardif 1994), actively suppressed the reproduction of subdominant females (Barrett et al. 1990; Savage et al. 1988). She was either monogamous (Epple & Katz 1980) or surrounded by multiple mates to whom the paternity of offspring was uncertain (Garber 1997; Sussman & Garber 1987; Sussman & Kinzey 1984). As further data were accumulated from wild populations however, the largely captive-study driven description of a typical callitrichid was found to be an insufficient explanation of their natural variability in the wild (Savage & Baker 1996). Today, rather than being an exception to the general image of a cooperatively breeding primate, behavioral flexibility in mating strategies is a hallmark feature of the Callitrichidae.

This flexibility is pervasive, affecting almost all aspects of demography and reproduction across species. We see numerous exceptions to single birth events in a group (Smith et al. 2001), most notably in the newly described genus *Callibella* that routinely raises more than one set of twin offspring (van Roosmalen & van Roosmalen 2003). This in turn brings into question strict reproductive suppression of subdominant females by the primary breeding female, and as expected, a range of levels of suppression have been observed in wild callitrichids (French et al. 2003; Löttker et al. 2004b). In fact, there is evidence of multiple paternities within the same pair of twin offspring among *S. mystax* in the wild (Löttker et al. 2004a).

Callitrichids exhibit a wide range of mating systems, which are centered on the premise that certain individuals in a population have the ability to control the access of others to prospective mates, making mate availability unequal across a population (Emlen & Oring 1977). Their mating strategies are dependent on their ecology and demography, as well as the physiology of individual animals within the species (Garber et al. 1993; Löttker et al. 2004a; Terborgh & Goldizen 1985). In a population of saddleback tamarins studied for over 13 years at Cocha Cashu in Peru, all feasible mating systems – polyandry, polygynandry, polygyny and monogamy – were observed (Goldizen et al. 1996). Each group also exhibited variable mating systems across time. Such flexibility within a single group of callitrichids suggests a complex interaction between physiology, demography and ecology in these primates.

Given the difficulty of raising twin offspring, and the necessity for assistance from the group, ideal breeding opportunities are rare among callitrichids (Garber et al. 1993; Goldizen et al. 1996; Löttker et al. 2004a; Terborgh & Goldizen 1985). The reproductive success of a given individual is dependent not only on the availability of breeding opportunities, which might be determined by the effects of stochastic environmental factors on demography , but also on the physiological capability of an individual to attract a mate, copulate, give birth and raise its offspring. Identifying the factors that suggest fertility, or a capability for reproduction, is then paramount to recognize the breeding status of individuals. Mating itself is a cryptic behavior among callitrichids (Garber et al. 1993; Löttker et al. 2004b; Terborgh & Goldizen 1985), easily missed by even a practiced observer, thus rendering behavioral observations alone ineffective in the determination of the breeding status of every individual in a group.

I provide a mechanism for determining the breeding status of an individual callitrichid may be identified from its age and morphology, in conjunction with observed reproductive behavior. I examine the morphological variables reflecting underlying physiology that allows an animal to occupy a coveted breeding position in a group. I also examine mating behavior and

seasonal breeding differences between the two species of callitrichids in this chapter, and ascertain if certain mating systems reliably produce higher reproductive outputs in this population. With this comprehensive knowledge of breeding status and mating systems of both species at this site, we can then establish, in the next chapter, if demographic variables and ecological stochasticity facilitate the acquisition of breeding status among young callitrichid primates.

VI. 2: Methods

VI. 2. 1: Study Population

Over the course of three trapping seasons, we captured and marked 57 *Saguinus fuscicollis* (in 7 groups) and 36 *S. imperator* (in 6 groups). Each tagged group was recaptured every year, with only one exception (SF5 was not recaptured in 2011 due to a time restriction). We observed groups of *S. fuscicollis* for 19 non-consecutive months, and for 13 of those months, we also monitored groups of *S. imperator*. We record certain statistics at fixed times during the year (either April at the beginning of the field season, or August at the end of the season) to serve as a comparison for similar annual statistics calculated at other sites (Garber et al. 1993; Goldizen et al. 1996; Löttker et al. 2004a)

VI. 2. 2: Measuring Individual Characteristics

Individuals were scored on the basis of molar occlusal wear and dental eruption schedules, to determine age-classes, as described in Chapter IV. Morphometric data, including reproductive measures such as testicular volume and vulvar indices, were measured on each individual (described in detail in Chapter V). Further, a scoring key was created for visible pigmentation of the genitalia and suprapubic scent glands, and each individual scored based on photographic evidence obtained every time they were captured (Chapter V). It must be noted here that all morphometric data were recorded several months after individuals had given birth, since the annual capture program is conducted in the dry season, when infants are between 3

and 6 months old. Pregnant females are not expected during any captures, and if present were only in their first month of pregnancy.

VI. 2. 3: Reproduction

One dataset of mating behavior contains instances from both tagged and untagged groups across the full study period for both species. A second dataset consists only of mating observed in tagged groups (where the identities of the individuals are known) – this allows us identification of individual differences in mating behavior and some, if not all, reproductively active individuals. Mating behavior was recorded during follows of specific groups during the following periods: December 2009 to July 2010 (marked groups of *S. fuscicollis*) and July and August 2012 (marked groups of both species, SF1 and SI3). Most, if not all, mating instances were observed during these times, with the exception of 2011, during which time data are under-sampled for Group SI3. For both data sets, several features were noted for each mating incident: duration, occurrence of intromission (at all, never, or some of the time), and the reaction of the female to the male.

We calculated reproductive output (number of infants) per group for every year that it was observed (14 group years in the case of *Saguinus fuscicollis,* and 13 group years in the case of *S. imperator*). We then took the mean value across all groups in a particular field season to determine the average reproductive output of groups of a species in a given year. Reproductive output here does not reflect the number of infants born each year, since groups were only assessed when infants were at least 4-6 mo old (infants that died before that time would not be observed).

VI. 2. 4: Births and Breeding Seasons

Two infant *Saguinus fuscicollis* were born during the study, and the exact date of birth is known. I noticed that these individuals were younger than would be estimated by Glassman's (1983) schedule of dental eruptions (Chapter IV). This is likely to pertain to all estimations of

age for the other infants for whom only dental information is available. Therefore, where Glassman provided a range of ages, I used the lowest estimated age as the final chronological age for each animal (Chapter IV). From these estimated ages at the time of capture, birth seasons were then extrapolated for each species. We conducted detailed behavioral observations on group SF1 from December 2009 to July 2010. During this time, observations led us to suspect that multiple breeding females might exist in this group, so mating and nursing behaviors were specifically evaluated in this group.

VI. 2. 5: Breeding Status

We used visual observations of nursing to identify the mothers of offspring in a group. For these known breeding individuals, we gathered information on the following reproductive variables (RV) (from Chapters IV and V): vulvar key score, suprapubic gland key score, vulvar index, suprapubic gland area, nipple length and age category (or known age, where possible). Using observed instances of reproductive activity as a guide, we determined if the RVs of all other females in our dataset fell within two standard deviations of the mean RV values for breeding individuals.

For males we used the following RVs: scrotal key score, suprapubic gland key score, testicular volume, suprapubic gland area, and age category (or known age, where possible) (from Chapters IV and V). Since paternity is impossible to verify without genetic data given multiple possible fathers, we had to assign confirmed breeding status only to males who were observed mating. This is necessarily an underestimation of all breeding males in the population since all groups were not followed intensively, and mating instances from only a few groups are known; however, an adequate pool of breeders was identified in this way. Subsequently, the RVs of males of unknown status were compared to known breeding males, using similar methods as with females.

In this manner, every individual is known to either fall within or outside the range of values of known breeding individuals of the same sex. We make the assumption that individuals born in the same year as the study i.e. of the infant age-class are by definition non-breeding individuals. Each group's members in a given year were examined for the similarity of their RVs to known breeders, records of mating behavior, and reproductive and demographic events that occurred that year. The results of this examination allow us to confirm the breeding status assignation for each individual every year. Subsequently, we suggest guidelines for the classification of an individual's breeding status based on the range of values for the RVs we observed in each category.

VI. 3: Results

VI. 3. 1: Births

A total of 18 infant *S. fuscicollis* were observed over 14 group-years, for an average overall reproductive output of 1.2 infants per group per year. In the case of *S. imperator*, 11 infants were observed over 13 group-years, with an average reproductive output of 0.85 infants per group per year (Table VI. 1A). Mean reproductive output per group of *Saguinus fuscicollis* was 1 infant/group from 2009-2011, and 1.5 infants/group in 2012 (Table VI. 1A). *Saguinus imperator* maintained a reproductive output of *ca.* 0.8 infants per group during both 2011 and 2012. Reproductive output is based on infant survival to 4 – 6 mo of age and not birth rates.

Both twins and singletons were observed in both species. The average twinning rate was 0.6 twin pairs per group per year in *S. fuscicollis*, and 1.0 pair per group per year in *S. imperator*. Singletons born to *S. fuscicollis* could have experienced mortality of a sibling and cannot be confirmed. All groups of *S. fuscicollis* reproduced at least once during the study, whereas 3 of the 7 groups of *S. imperator* were not observed to reproduce at all (Table VI. 1B). Only one group of *S. imperator* successfully raised both twin infants every year of the study, others only had twins in some years (Table VI. 1B).

VI. 3. 2: Mating Behavior

We observed 116 instances of mating or attempted mating (mounting) by *S. fuscicollis* across the study, and only 13 such instances by *S. imperator*. Sampling inequality between species exists, since focal follows of only *S. fuscicollis* were conducted over 10 months in 2009 and 2010. In July and August 2012, when both species were evenly sampled, we observed 15 instances of mounting by *S. fuscicollis* and 10 in *S. imperator*.

When there was intromission during mating, it typically lasted the entire event; males either were successful or not, and transitory events that were partially successful were not observed. Mating attempts resulted in successful intromission 70% of the time in *S. fuscicollis* and 77% of the time in *S. imperator* (Fig. VI. 1). When intromission occurred, mating lasted for an average of 13 s in *S. fuscicollis* (range: 1- 60 s), and 12 s in *S. imperator* (range: 2 to 24 s). Female responses to the mating attempt by the male often included positive (acceptance of male) and negative (rejection by moving away, lunging, or aggression) attitudes in quick succession. The female response was difficult to classify consistently. No female was ever observed to solicit mating from a male and all approaches to mating were made by the males. An extremely emphatic attempt at mate-guarding was observed in Group SI3, which had three adult males and one infant male to a single adult female in 2012. The males never left the side of the female for several days, stalking her every move and constantly bickering between themselves over access to the female.

VI. 3. 3: Birth Seasons

Births were estimated to occur from August to February in *Saguinus fuscicollis* and from November to March in *S. imperator*. No infants were captured that were born in any other time of the year. Births were seasonal in both species (occurring during the wet season), with > 2 birth events each in October, December and January in *S. fuscicollis* and the same only in November and December in *S. imperator* (Fig. VI. 3, Table VI. 3); in fact, all but one birth event

among *S. imperator* occurred in November and December. The outlier occurred in March, and produced twins, one of which did not survive to the following year (Fig. VI. 4).

VI. 3. 4: Nursing and Weaning

In November 2009, F11, an adult female *S. fuscicollis* in focal group SF1 gave birth to infants. A second older adult female (F10) was present in the group. The twin infants were first nursed by their mother F11, for 109 days (*ca*. 3.6 mo), of which the last 30 days contained attempts at weaning (Fig. VI. 5). These weaning behaviors included removing the twins from the breast instead of letting them stop nursing naturally, and eventually rejection of the twins when they approached to nurse. From day 109 to day 234, for 125 days (*ca*. 4.2 mo), F10 allonursed the infants (Fig. VI. 5). During *ca*. last 50 days of this period, weaning behaviors were exhibited by F10.

Table VI. 1A: Reproductive output across the study period for each tamarin species

Time Period	# birth events	# infants born	# groups tagged	# birth events/ group	# infants born/ group
Saguinus fuscicollis			**Average =**	**0.8**	**1.2**
2009-2010	3	5	5	0.6	1.0
2010-2011	2	4	4	0.5	10
2011-2012	7	9	6	1.2	1.5
Saguinus imperator			**Average =**	**0.5**	**0.8**
2010-2011	3	5	6	0.5	0.8
2011-2012	3	6	7	0.4	0.9

Birth event = a single birth, irrespective of number of infants born

Table VI. 1B: Mean reproductive output (i.e. average number of infants) of each group across the study period

Group	*Reproductive Output*	Group	*Reproductive Output*
SF1	1.33	SI1	1.00
SF2	1.00	SI2	2.00
SF3*	2.00	SI3	0.00
SF4	1.33	SI4	1.00
SF5	1.33	SI5a	0.00
SF6*	1.00	SI5b*	0.00
SF7*	1.00	SI6*	2.00

SI = *Saguinus imperator*; SF = *Saguinus fuscicollis*

Reproductive output calculated over 3 years for *S. fuscicollis* and 2 years for *S. imperator*. Note: *SF3 only survived one year so reproductive output for that year is presented; SF6, SF7, SI5b & SI6 were also only monitored for 1 year

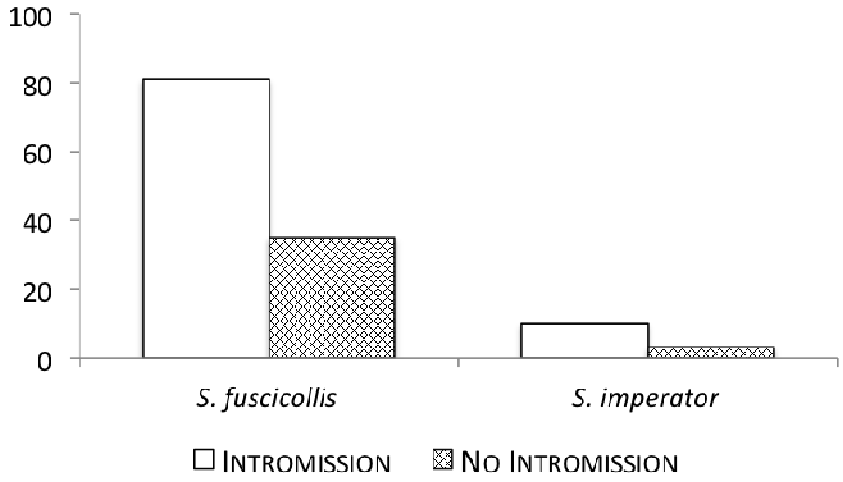


Figure VI. 1: Mating attempts in both species over the full study, isolated into instances with and without successful intromission. Mating events classified exclusively as either "intromission" or "no intromission" based on whether the event contained any intromission at all, since typical successful events included intromission for the majority of the duration of the event.

Table VI. 2: Mating pairs observed during the study for both species with number of instances of mating in parentheses.

Group	Individual	2009	2010	2011*	2012
SF1	F10	M11(2),M10(1)	M10 (25)	Dead	Dead
SF1	F11	M10 (1)	M10 (19)	M10 (2)	M12(9),M14(6)
SF1	F13	Infant	Infant	Young Adult	M12(5),M14(6)
SF2	F22			Unk. male (1)	M21 (1)
SF4	F41			M40 (1), M42 (1), M43 (1)	M42 (1)
SF7	F72				M73 (1)
SF7	F71				M52 (1)
SI3	F30			M31 (1)	M32 (4), M61 (4), M33 (1)
SI4	F40			M41 (1)	Unk. male (1)
SI5	F50				M51 (1)

SF = *Saguinus fuscicollis*; SI = *Saguinus imperator*; M = Male; F = Female

* 2011 data was under-sampled so other instances of mating could have occurred that we missed. 2009, 2010 and 2012 data is comprehensively sampled.

Note: SIM33 is a young male infant who successfully mated with SIF30, the primary breeding female, who was not his mother.

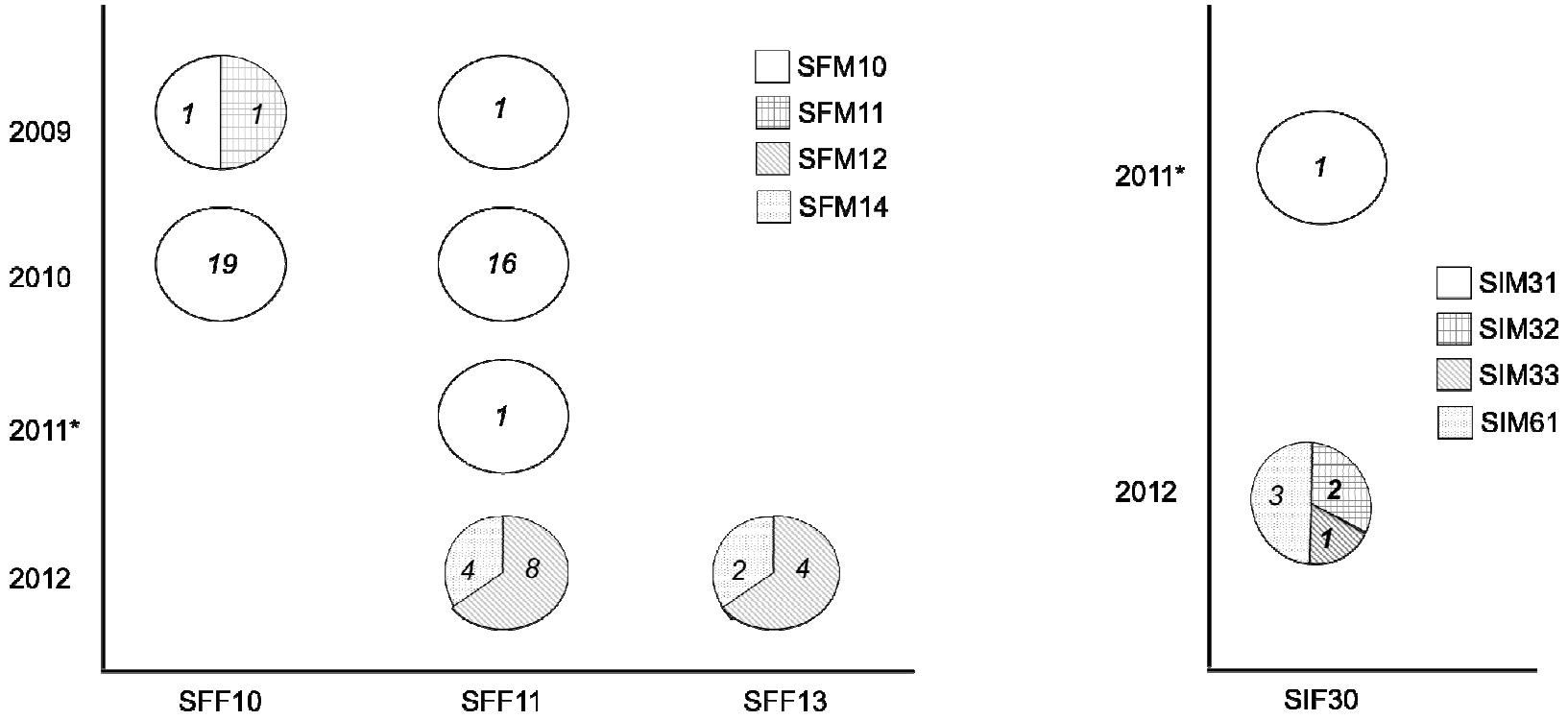


Figure VI. 2: Observed mating attempts of females by males that included any intromission for group SF1 (left) and SI3 (right).

* Data from 2011 are under-sampled and likely could be missing mating instances by other males or females. During all other data years, comprehensive follows were conducted on both groups.

Female F11's nursing and weaning period coincided with a possible pregnancy of F10. During her nursing period (*ca*. 2.6 mo), F11 mated 3 times, mostly toward the end of the period (rate = 1.2 mating events/mo). During the weaning period (*ca*. 1 mo) she mated 4 times, which is at a rate 3.5 times higher than during nursing. After weaning, during the next 4.5 mo, she mated at a rate of 2.4 mating events per month, but did not give birth in 2011 (Fig. VI. 5).

Female F10 took over nursing on day 109 since birth, and is presumed to have been pregnant before this time, resulting in a miscarriage or still-births but the ability to lactate. During this likely pregnancy she was observed for *ca*. 3.7 mo and mated at a rate of 1.9 mating events a month. During her nursing period (*ca*. 2.5 mo) she mated at a rate of 0.4 events per month, concentrated between day 180 and 190. While weaning, her mating rate was 4.8 events per month, and subsequently, 11 events per month (4 times in 11 days) (Fig. VI. 5). She disappeared and was presumed dead in 2011 because of her older age class.

Table VI. 3: Infant births and survivorship of *Saguinus fuscicollis* and *Saguinus imperator* across the study period.

ID	Estimated Birth	Age (mo)	Survival for 1 year	Comments
Saguinus fuscicollis				
F12	November, 2009	7 ¼	Yes	Dispersing by 30 mo of age
F13	November, 2009	7 ¼	Yes	SBF in natal group at 30 mo
F14	September, 2011	7 ¼	TBD	F14 and F15 display unequal development (F14 slightly older than F15), survived to *ca*. 10 mo
F15	October, 2011	8	TBD	
F23	January, 2010	3	Yes	In natal group at 30 mo of age
F24	January, 2010	3	Dead	Disappeared from group by 2011
M22	January, 2012	5 ¾	TBD	Survived to minimum of 7 mo
M32	December, 2009	4 ½	Dead	Died during July 2010 *friaje*
M33	December, 2009	4 ½	Dead	Died during July 2010 *friaje*
M43	October, 2010	5 ¾	Yes	In natal group at 21 mo of age
F43	October, 2010	5 ¾	Yes	In natal group at 21 mo of age
M44	September, 2011	9 ¾	TBD	Survived to minimum of 10 mo

Table VI. 3: ***Continued***

ID	Estimated Birth	Age (mo)	Survival for 1 year	Comments
M45	September, 2011	9 ¾	TBD	Survived to minimum of 10 mo
M51	January, 2010	5 ¾	Yes	In natal group at 30 mo of age
F53	November, 2011	7 ¼	TBD	Survived to minimum of 8 mo
F60	September, 2011	9 ½	TBD	Survived to minimum of 10 mo
M71	September, 2011	9 ¾	TBD	Survived to minimum of 10 mo
M72	January, 2011	5 ¾	TBD	Survived to minimum of 6 mo
Saguinus imperator				
M12	November, 2011	7 ¼	TBD	Survived to minimum of 8 mo
M13	November, 2011	7 ¼	TBD	Survived to minimum of 8 mo
F21	March, 2011	1 ½	Yes	Dispersal attempts at 17 mo of age
M23	March, 2011	1 ½	Dead	Disappeared from natal group
F22	November, 2011	7 ¼	TBD	Survived to minimum of 8 mo
F23	November, 2011	7 ¼	TBD	Survived to minimum of 8 mo
F32	November, 2011	7 ¼	Unk.	Disappeared, possibly dispersed
M33	November, 2011	7 ¼	TBD	Survived to minimum of 8 mo
F40	November, 2010	5 ¼	Dead	Disappeared from group by 2012
F43	November, 2010	5 ¼	Yes	In natal group at 20 mo of age
F51	November, 2010	5 ¾	Yes	Died soon after second capture

M = Male; F = Female

TBD = To be determined in the future; Unk. = Unknown; SBF = Secondary breeding female

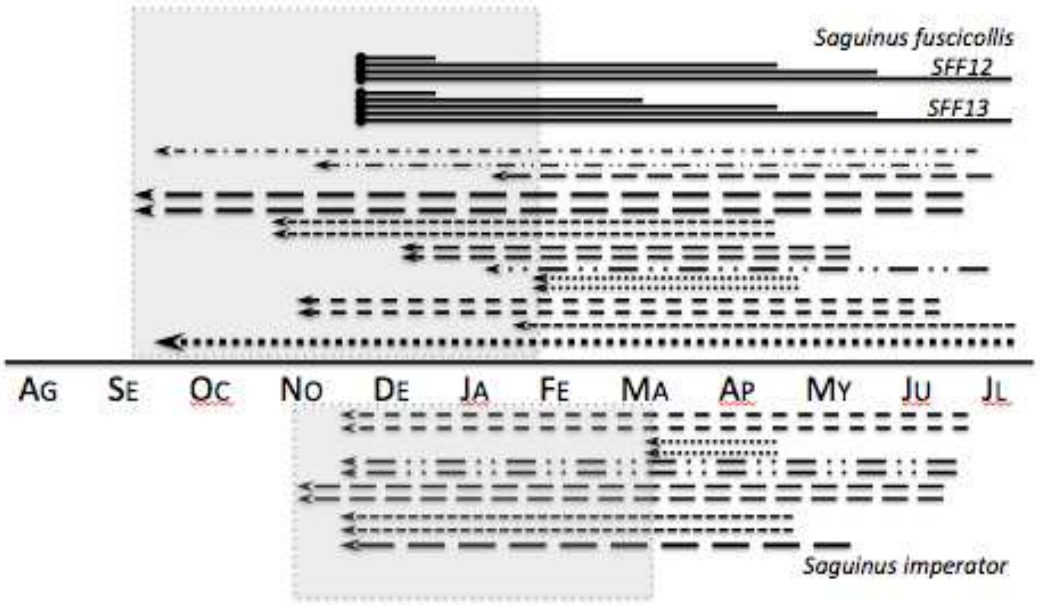


Figure VI. 3: Birth seasons predicted from individuals of known age identified through dentition analyses in Chapter IV. The arrows run from the point of trapping backwards till the estimated birth. Births of *Saguinus fuscicollis* are presented above the scale and below it are births of *Saguinus imperator*. The two infants with an observed birth event (SFF12 and SFF13) were trapped multiple times and their ages evaluated, indicated especially at the top. Each arrow represents a single infant, with twin siblings depicted by identical line patterns. The time period encompassing the earliest and latest birth events for each species are highlighted with grey shading: mid-September to late January for *S. fuscicollis* and early November to early March for *S. imperator*.

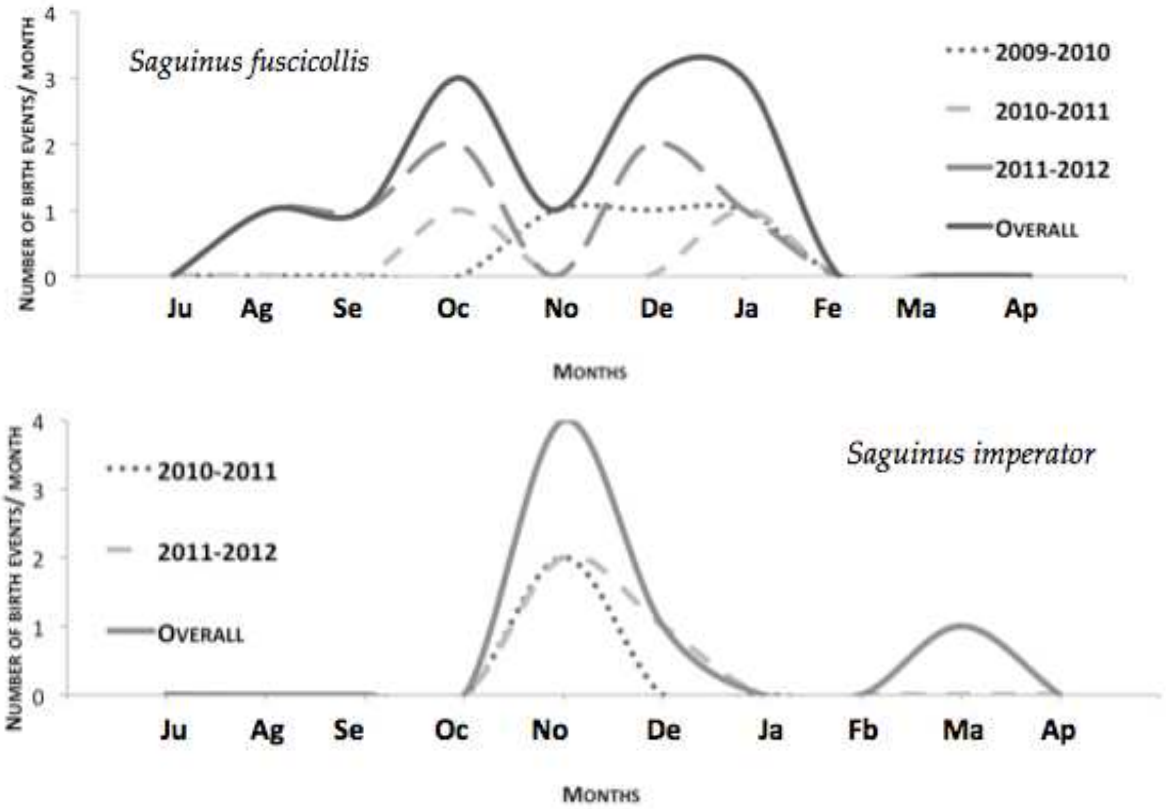


Figure VI. 4: The number of birth events per month for each species. Seasonal births are evident for each species. Most births occur in October, December and January for *Saguinus fuscicollis*, while the majority of births occur during November in *Saguinus imperator*. Note: Infants that died at birth or were not observed by observers due to a short lifespan are not included in these analyses and could skew this chart to some extent.

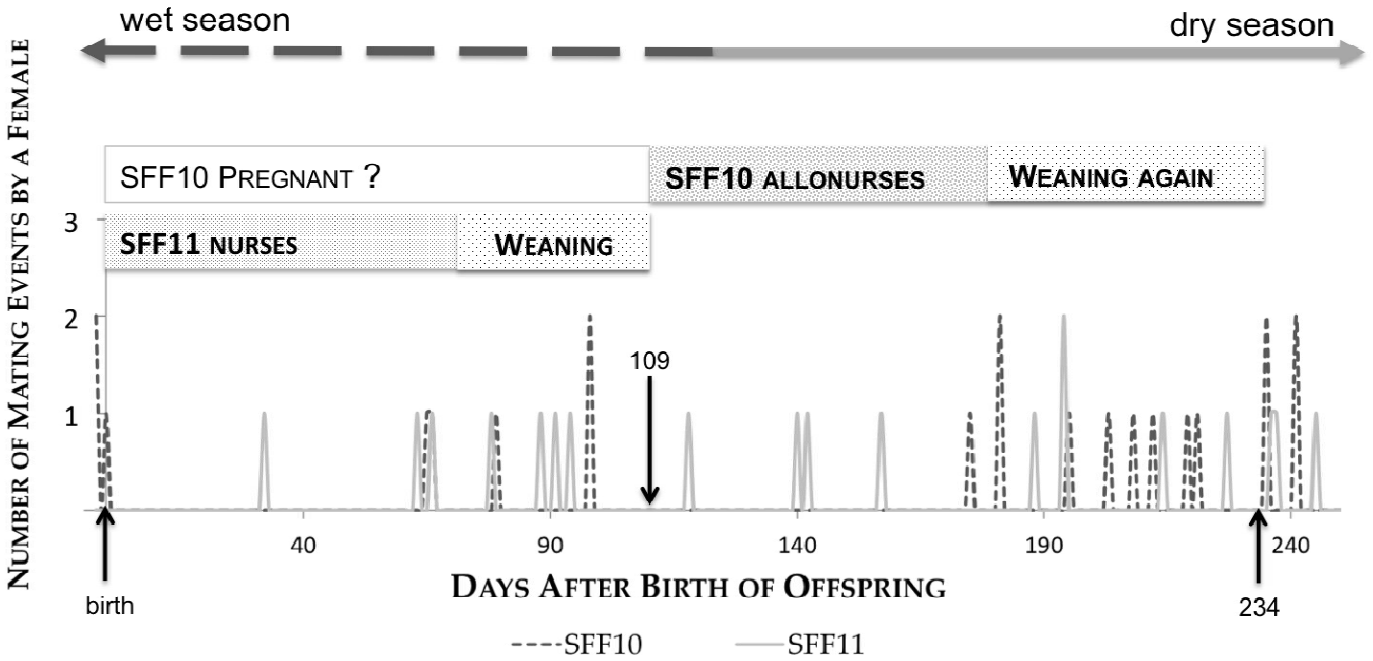


Figure VI. 5: Mating instances of breeding females (SFF10, SFF11) in Group SF1 during 8 months of observation in 2009 and 2010. Observed nursing behavior is depicted as horizontal bars above the graph. Weaning behaviors include rejections of infants when they attempt to nurse. Weaning coincides with increased mating in the group for the female involved, while nursing coincides with reduced mating instances for that female. Unusually in this group, we observe allonursing of infants by one female (SFF10), even though they were not biologically hers, indicating a possible unsuccessful pregnancy.

Zero on the horizontal axis = 11/23/09, the birthday of twin offspring to SFF11.

Day 109 = first day SFF10 nursed infants

Day 234 = last day SFF10 nursed infants

VI. 3. 5: Recommended Guidelines for Breeding Status

Guidelines to allocate breeding status based on this population differ for each sex, and by species as follows:

Female *Saguinus fuscicollis* (Tables VI. 4 and VI. 5)

- Primary breeding females are those that a) are observed nursing offspring or b) in the absence of nursing data, are the only female in the group with average nipple lengths ≥ 3.0 mm, which implies parity and c) with vulvar indices generally ≥ 19 mm, suprapubic gland scores of 5 or 6
- Secondary breeding females always have vulvar scores are ≤ 3, suprapubic gland scores ≤ 4, and nipple lengths < 3.0 mm. They also have vulvar indices ≥ 16 mm or observed instances of mating.

Male *Saguinus fuscicollis* (Tables VI 6. and VI. 7)

- Breeding males are those with testicular volumes ≥ 500 mm^3 and scrotal and glandular scores of 3, 4 or 5.
    - Exceptions include older adult males with reduced testicular volumes but observed mating records.
- Primary breeding males always have testicular volumes ≥ 730 mm^3 or were seen to mate with a female.
- Secondary breeding males always have testicular volumes ≥ 500 mm^3 and ≤ 730 mm^3, but have not been seen to mate.
- Note: Since observed mating often causes a secondary breeding male to be considered a primary breeding male, and mating instances could be missed by observers, it appears that secondary and primary breeding males are not functionally distinct in this species, but do appear to fall into distinct classes based on reproductive scores and measures alone.

Female *Saguinus imperator* (Tables VI. 8 and VI. 9)

- Breeding females have vulvar indices ≥ 22 mm
- Primary breeding females always have average nipple lengths ≥ 4.0 mm, suprapubic gland areas ≥ 200 mm^2, and vulvar indices ≥ 22 mm. Their gland and vulvar key scores range from 2 to 4
- Secondary breeding females almost always are nulliparous (based on nipple length), with vulvar indices ≥22 mm but ≤ 25 mm, and suprapubic gland areas ≤ 170 mm^2

Male *Saguinus imperator* (Tables VI. 10 and VI. 11)

- Breeding males have testicular volumes ≥ 500 mm^3
- Primary breeding males have suprapubic gland areas ≥ 120 mm^2 and testicular volumes ≥ 700 mm^3, except in cases of older adults
- Secondary breeding males have testicular volumes between 500 and 700 mm^3, and either none or very small (≤ 100 mm^2) suprapubic glands

Table VI. 4: Reproductive measures and scores for all primary breeding females in groups of *Saguinus fuscicollis*

PBF	Year	Group	Age	Vulva Score	Gland Score	Vulva Index (mm)	Gland Area (mm^2)	Nipple Length	# SBFs	# Male Mates	Reprod. Output	Comments
F10	1	SF1	OAd	4	6	20	226	3.9	1?	3	2?	Nursed infants (March – June)
F11	1	SF1	Ad	3	5	20	133	3.9	1?	3	2?	Nursed infants (December–March) lowest suprapubic gland area, 2.7 yrs old
F21	1	SF2	Ad	5	6	25	393	0	1	2	0	Both females die after a *friaje*
F31	1	SF3	Ad	5	6	23	379	5.6	0	2	2	Group dies after a *friaje*
F41	1	SF4	YAd	4	6	28	484	0	0	3	0	Highest suprapubic gland area
F50	1	SF5	Ad	5	6	24	263	**	1?	2	1?	Two likely PBFs
F51	1	SF5	Ad	5	5	20	265	3.7	1?	2	1?	Two likely PBFs
F11	2	SF1	Ad	-	-	-	-	-	0	1	0	Not trapped this year, 3.4 yrs old
F22	2	SF2	Ad	4	5	22	283	4.3	0	2	2	
F41	2	SF4	YAd	4	6	28	483	0	0	3	2	Highest suprapubic gland area
F50	2	SF5	Ad	-	-	-	-	-	2?	3	2?	Two likely PBFs
F51	2	SF5	Ad	-	-	-	-	-	2?	3	2?	Two likely PBFs
F11	3	SF1	Ad	3	5	19	157	4.0	1	2	2	Lowest vulvar index, 4.6 yrs old
F22	3	SF2	Ad	-	-	-	-	-	0	2	1	
F41	3	SF4	OAd	4	6	23	415	4.4	1	3	2	
F50	3	SF5	Ad	5	6	24	311	3.0	1?	3?	0	Two likely PBFs
F51	3	SF5	Ad	-	-	-	-	-	1?	3?	0	Two likely PBFs, not trapped
F61	3	SF6	Ad	5	6	29	341	3.0	0	1	1	Highest vulvar index
F70	3	SF7	OAd	4	5	23	265	4	2?	3	1	PBF with one infant
F71	3	SF7	Ad	5	6	22	341	3.4	2?	3	1	PBF with one infant

PBF = Primary Breeding Female; SBF = Secondary Breeding Female; OAd = Older adult; Ad = Adult; YAd = Young adult;
**Measurement not taken; ? = Uncertainty as to the number of primary vs. secondary breeding individuals there are in the group

Table VI. 5: Reproductive measures and scores for all secondary breeding females in groups of *Saguinus fuscicollis*

SBF	Year	Group	Age	Vulva Score	Gland Score	Vulva Index (mm)	Gland Area (mm^2)	Nipple Length	PBF	Fertility	Parity	Comments
F20	1	SF2	Ad	1	3	16	95	0	F21	Likely	Nulliparous	
F13	3	SF1	Ad	3	2	21	166	0	F50	Likely	Nulliparous	30 mo of age
F43	3	SF4	Ad	2	4	25	133	*	F60	Likely	Unknown	Nipple length measurement is missing, so parity cannot be assessed; 20 mo of age
F72	3	SF7	Ad	3	4	19	299	0	F70	Likely	Nulliparous	

SBF = Secondary Breeding Female; PBF = Primary Breeding Female

Fertility = Likely if vulvar index is > or close to 19

Parity = Nulliparous if nipple length is ≥ 3.0 mm

Table VI. 6: Reproductive measures and scores for all primary breeding males in groups of *Saguinus fuscicollis*

PBM	Year	Grp	Age	Scrot Score	Glnd Score	TVol. (mm^3)	Gld Area (mm^2)	Tot. # mates	Mated with	Shared mates with	Comments/ Paternity
M10	1	SF1	UNK	3	5	1458	132	2	F10, F11	M11, M12	
M11	1	SF1	OAd	5	4	443	*	2	F10	M10, M12	OAd: TVol. reduced
M12	1	SF1	Ad	5	4	994	*	2	Not Seen	M10, M11	
M21	1	SF2	Ad	5	5	550	*	2	Not Seen	M20	Male with highest TVol.
M30	1	SF3	OAd	4	4	824	82	1	Not Seen	M31	
M31	1	SF3	Ad	3	3	730	102	1	Not Seen	M30	
M40	1	SF4	Ad	5	3	1087	*	1	Not Seen	M41, M42	
M41	1	SF4	Ad	3	3	1042	23	1	Not Seen	M40, M42	
M52	1	SF5	Ad	4	4	875	113	2	Not Seen	M50	
M10	2	SF1	Ad	3	5	761	135	1	F11	No one	
M20	2	SF2	Ad	4	4	1145	105	1	Not seen	M21	
M21	2	SF2	*	*	*	*	*	1	Not seen	M20	
M40	2	SF4	Ad	*	*	*	*	1	F41	M41, M42	
M41	2	SF4	Ad	*	*	837	54	1	Not seen	M40, M42	
M52	2	SF5	*	*	*	*	*	2	Not seen	M50	
M13	3	SF1	Ad	3	5	1241	177	2	F11, F13	M14	
M14	3	SF1	Ad	4	4	1325	120	2	F11, F13	M13	
M20	3	SF2	Ad	4	4	1072	102	1	Not seen	M21	
M21	3	SF2	Ad	4	4	895	93	1	F22	M20	
M41	3	SF4	Ad	4	4	1287	87	2	Not seen	M42, M43	
M42	3	SF4	Ad	3	4	1353	76	2	F41	M41, M43	
M50	3	SF5	Ad	4	4	875	113	2	Not seen	M51, M52	
M51	3	SF5	Ad	4	4	907	75	2	Not seen	M50, M52	
M52	3	SF5	Ad	4	5	1503	183	2	F71	M50, M51	
M60	3	SF6	Ad	2	5	1232	309	1	Not seen	No one	
M70	3	SF7	Ad	3	4	860	106	3	Not seen	M73, M74	
M73	3	SF7	Ad	3	4	1119	237	3	F72	M70, M74	
M74	3	SF7	OAd	4	4	793	120	3	Not seen	M70, M73	

PBM = Primary Breeding Male; Grp = Group Name; Scrot Score = Scrotal Score (chapter V); Glnd Score = Suprapubic gland score (chapter V); TVol. = Testicular volume (mm^3); Gld Area = suprapubic gland area (mm^3);

Tot # mates = Total number of fertile females (primary or secondary breeding females) available to mate with

Mated with = The IDs of females observed mating with the male in question. Note: Mating is a rare behavior so the absence of evidence here is not evidence of nonbreeding status

Shared mates with = The IDs of reproductively active males that share access to the fertile females in a group, with whom mating opportunities must be shared or competed for

* Measures not available because animals were either not captured that season (as is the case with Group SF5 in 2011) or specific measurements were not recorded due to time constraints during capture

Table VI. 7: Reproductive measures and scores for all secondary breeding males in groups of *Saguinus fuscicollis*

SBM	Year	Grp	Age	Scrot Score	Glnd Score	TVol. (mm^3)	Gld Area (mm^2)	Tot. # mates	Mated with	Shared mates with	Comments/ Paternity
M42	1	SF4	Ad	3	4	687	75	1	Not seen	M40, M41	
M50	1	SF5	Ad	4	4	581	77	2	Not Seen	M52	
M42	2	SF4	Ad	3	4	322	114	1	F41	M40, M41	Only included as mating was observed
M50	2	SF5	Ad	*	*	*	*	2	Not Seen	M51, M52	Not trapped, measures unknown
M51	2	SF5	Ad	*	*	*	*	2	Not Seen	M50, M52	Not trapped, measures unknown
M43	3	SF4	Ad	2	2	662	0	2	Not Seen	M41, M42	

SBM = Secondary Breeding Male; Grp = Group Name; Scrot Score = Scrotal Score (chapter V); Glnd Score = Suprapubic gland score (chapter V); TVol. = Testicular volume (mm^3); Gld Area = suprapubic gland area (mm^3);

Tot # mates = Total number of fertile females (primary or secondary breeding females) available to mate with

Mated with = The IDs of females observed mating with the male in question. Note: Mating is a rare behavior so the absence of evidence here is not evidence of nonbreeding status

Shared mates with = The IDs of reproductively active males that share access to the fertile females in a group, with whom mating opportunities must be shared or competed for

* Measures unavailable because animals were not captured that year (Group SF5 in 2011)

Table VI. 8: Reproductive measures and scores for all primary breeding females in groups of *Saguinus imperator*

PBF	Year	Group	Age	Vulva Score	Gland Score	Vulva Index (mm)	Gland Area (mm^2)	Nipple Length	# of SBFs	# Male Mates	Reprod. Output	Comments
F10	1	SI1	YAd	4	4	24	295	0.0	0	1	0	Nulliparous
F20	1	SI2	YAd	3	3	31	198	7.5	0	3	0	Lowest suprapubic gland area
F30	1	SI3	OAd	3	3	32	254	5.0	0	3	0	
F41	1	SI4	Ad	4	2	21	121	4.5	0	2	0	Two breeding females
F42	1	SI4	Ad*	2	2	25	213	4.2	0	2	2	Two breeding females
F50	1	SI5	Ad	4	2	22	217	4.7	1	2	2	Lowest vulvar index
F60	1	SI6	YAd	4	4	27	207	4.3	1	2	0	
F10	2	SI1	Ad	4	2	30	214	4.8	0	2	2	
F20	2	SI2	Ad	-	-	-	-	-	0	2	2	Not trapped this year
F30	2	SI3	OAd	3	3	33	345	4.9	0	3	0	Highest suprapubic gland area and vulvar index
F42	2	SI4	Ad	4	4	28	330	4.6	0	1	0	
F50	2	SI5	Ad	4	3	26	270	4.6	0	1	0	

PBF = Primary Breeding Female; SBF = Secondary Breeding Female

Year 1 = 2011; Year 2 = 2012; Reproductive Output = all infants thought to be offspring of the primary breeding female in question

* Probably an adult but the dental cast was badly damaged during transport.

Male Mates: include primary and secondary breeding males i.e. any male capable of reproductive activity regardless of testicular volume. In some cases, males were actually observed mating, but since it is impossible to be sure that all mating instances are witnessed, this is not the only criteria for qualifying for breeding status.

Table VI. 9: Reproductive measures and scores for all secondary breeding females in groups of *Saguinus imperator*

SBF	Year	Group	Age	Vulva Score	Gland Score	Vulva Index (mm)	Gland Area (mm^2)	Nipple Length	PBF	Fertility	Parity	Comments
F51	1	SI5	Ad	3	2	21	166	3.7	F50	Likely	Unlikely	
F61	1	SI6	Ad	2	4	25	133	-	F60	Likely	Unknown	

SBF = Secondary Breeding Female; PBF = Primary Breeding Female

Gland Score ad Gland Area refer to the suprapubic gland

Table VI. 10: Reproductive measures and scores for all primary breeding males in groups of *Saguinus imperator*

PBM	Year	Grp	Age	Scrot Score	Glnd Score	TVol. (mm^3)	Gld Area (mm^2)	Tot. # mates	Mated with	Shared mates with	Comments/ Paternity
M11	1	SI1	Ad	4	3	1052	*	1	Not Seen	No one	Gland not measured
M21	1	SI2	Ad	4	2	1036	*	1	Not Seen	M20, M22	Gland not measured
M30	1	SI3	Ad	3	2	753	0	1	Not Seen	M31, M32	
M31	1	SI3	Ad	2	4	317	143	1	F30	M30, M32	Lowest TVol., but included because he attempted to mate with the PBF
M40	1	SI4	*	*	*	*	*	2	Not Seen	M41	Not trapped in 2011
M50	1	SI5	*	2	2	1144	0	2	Not Seen	M51	Dental cast damaged in 2011
M51	1	SI5	YAd	2	3	1016	149	2	Not Seen	M50	
M60	1	SI6	Ad	2	2	759	123	2	Not Seen	M61	
M50	2	SI1	Ad	2	3	1147	175	1	Not Seen	M10	
M20	2	SI2	OAd	2	2	923	0	1	Not Seen	M22	
M32	2	SI3	OAd	5	2	765	0	1	F30	M61, M30	
M61	2	SI3	Ad	5	2	874	144	1	F30	M32, M30	Post dispersal to SI3
M30	2	SI3	OAd	3	2	510	124	1	Not Seen	M32, M61	Reduced Tvol likely due to age
M40/1	2	SI4	*	*	*	*	*	1	Not Seen	No one	Not trapped in 2012
M51	2	SI5	Ad	*	*	*	*	1	F50	No one	Not trapped in 2012
M60	2	SI6	Ad	3	2	712	160	0	-	M61	Loss of PBF, group splintered
M61	2	SI6	Ad	5	2	874	144	0	-	M60	Loss of PBF, successfully dispersed to SI3

PBM = Primary Breeding Male; Grp = Group Name; Scrot Score = Scrotal Score (chapter V); Glnd Score = Suprapubic gland score (chapter V); TVol. = Testicular volume (mm^3); Gld Area = suprapubic gland area (mm^3);

Tot # mates = Total number of fertile females (primary or secondary breeding females) available to mate with

Mated with = The IDs of females observed mating with the male in question. Note: Mating is a rare behavior so the absence of evidence here is not evidence of nonbreeding status

Shared mates with = The IDs of reproductively active males that share access to the fertile females in a group, with whom mating opportunities must be shared or competed for

* Measures unavailable because animals were not captured that year

Table VI. 11: Reproductive measures and scores for all secondary breeding males in groups of *Saguinus imperator*

SBM	Year	Grp	Age	Scrot Score	Glnd Score	TVol. (mm^3)	Gld Area (mm^2)	Tot. # mates	Mated with	Shared mates with	Comments/ Paternity
M20	1	SI2	OAd	2	1	654	*	1	Not Seen	M21, M22	
M22	1	SI2	*	3	3	561	*	1	Not Seen	M20, M21	
M32	1	SI3	*	*	*	*	*	1	Not Seen	M30, M31	Not trapped but likely breeding male since he bred for sure in year 2
M41	1	SI4	Ad	5	2	683	*	2	F40	M40	Tried to mate with infant F40, unsuccessful
M61	1	SI6	Ad	3	3	609	43	2	Not Seen	M60	
M10	2	SI1	Ad	3	1	635	60	1	Not Seen	M50	
M22	2	SI2	*	3	3	667	0	1	Not Seen	M20	

SBM = Secondary Breeding Male; Grp = Group Name; Scrot Score = Scrotal Score (chapter V); Glnd Score = Suprapubic gland score (chapter V); TVol. = Testicular volume (mm^3); Gld Area = suprapubic gland area (mm^3);

Tot # mates = Total number of fertile females (primary or secondary breeding females) available to mate with

Mated with = The IDs of females observed mating with the male in question. Note: Mating is a rare behavior so the absence of evidence here is not evidence of nonbreeding status

Shared mates with = The IDs of reproductively active males that share access to the fertile females in a group, with whom mating opportunities must be shared or competed for

* Measures unavailable because animals were not captured that year

VI. 3. 6: Characteristics of Breeding Individuals

I provide mean reproductive values for all identified breeders, including both known breeders as well as those individuals identified as possible breeders based on the mean reproductive values for the known breeders. While group compositions (single-male/single-female, single-male/multifemale, etc.) were assigned based on the number of adult individuals in a group, mating systems are assigned based on the number of breeding adults within a group. For example, monogamous groups contain only a single breeding adult male and female, irrespective of the number of adults present in the group. Mating systems, therefore, are based on the number of breeding adults identified as follows:

VI. 3. 6. 1: Female *Saguinus fuscicollis*

We identified 11 primary breeding females (PBF) over 20 capture instances during this study (Table VI. 4). They had a mean vulvar index of 23 mm ± 3 *SD* and mean suprapubic gland areas of 316 mm^2 ± 105 *SD*. All PBFs had suprapubic gland scores of 5 or 6 and vulvar scores of 3 to 5, indicating well-developed and pigmented glands and genitalia. We observed that 78.5% (11 of 14 instances) of the primary breeding females had given birth either that year or in the past, based on nipple lengths ≥ 3.0 mm (mean 3.9 mm ± 0.7 *SD*). The three nulliparous females also had the three highest suprapubic gland areas. In only 10% (2 of 20) of these instances were females in monogamous pairs, having access usually to 2 to 3 breeding males in their groups. In 65% (9 of 14) of these cases, primary breeding females were verified to have offspring. The oldest known PBF was 4.6 years old.

In 3 years, these females shared mating opportunities with fertile secondary breeding females, and in 7 years, they were the sole fertile females in their groups. In 5 years, there were possibly two primary breeding females within one group. First, group SF1 in 2010 appeared to have two primary breeding females, both of which gave birth, with only one set of offspring surviving; the second female allonursed this pair as well (Fig. VI. 5). In the second case, two

females with nearly identical high vulvar indices and suprapubic gland areas were observed in Group SF5 in all three years, and without observations of nursing, it was impossible to identify the mother of the single set of offspring raised by the group in each year with the current dataset (Table VI. 4). Finally, in Group SF7, two females are possible primary breeders and likely both gave birth to offspring because two infants were observed that were not siblings, based on their different age status or size.

We identified only four verifiable cases of secondary breeding females, with an average vulvar index of 20 mm ± 4 *SD*, and suprapubic gland area of 173 mm^2 ± 89 *SD*. All of these females appeared to be nulliparous, with vulvar and suprapubic gland scores displaying varying levels of development and pigmentation (Table VI. 5). Two of these females were 20 and 30 months old.

VI. 3. 6. 2: Male *Saguinus fuscicollis*

We assessed 18 primary breeding males over 28 capture instances (Table VI. 6). They displayed a mean testicular volume of 1008 mm^3 ± 270 *SD* and mean suprapubic gland areas of 121 mm^2 ± 63 *SD*. Their scrotal and suprapubic gland scores ranged from 3 to 5, showing a moderate range of development and pigmentation. Males had only one available breeding female in 43 % (12 of 28) of these instances, two available mates in 46% (13 of 28) of these instances, and 3 available female mates in only 11% of the cases (3 of 28). Of the 10 males observed mating, only 30% were seen mating with multiple females, although mating instances are likely to have been missed by observers in non-focal groups or focal groups on days they were not being observed (Table VI. 6).

Only 6 secondary breeding males were identified, with mean testicular volumes of 643 mm^3 ± 55 *SD* and suprapubic gland areas of 51 mm^2 ± 44 *SD* (Table VI. 7). Only one of these males was observed to mate with a female, which was the primary breeding female at the time. Both scrotal and suprapubic gland scores are low and highly variable. Males shared their mates

with two other breeding males in 54% of the cases (15 of 28), with one other breeding male in 39% of the cases (11 of 28) and with no other males in only 7% (2) of the cases (Table VI. 6).

Since evidence of mating can be used to promote secondary breeding males to primary breeding male status, both these groups should be regarded as potential mates for females. The distinction lies only in that two groups of males with differing testicular volumes were observed. In three cases of two-male groups, the single PBM had a testicular volume an average of 164% ± 122 *SD* larger than the SBM (range: 44 to 287% different). In an additional 3 cases of two-male groups, we saw two PBMs with a mean difference in testicular volume of 13% ± 7 *SD*. Three male groups contained either two PBMs and 1 SBM (2 cases, mean difference in testicular volume: 77% ± 32 *SD*) or three PBMs (3 cases, mean difference in testicular volume: 69%± 34 *SD*).

VI. 3. 6. 3: Female *Saguinus imperator*

We assessed 7 primary breeding females (PBF) over 12 capture instances during this study (Table VI. 8). These females displayed a mean vulvar index of 27 mm ± 4 *SD* and a mean suprapubic gland area of 242 mm ± 65 *SD*. Both vulvar and glandular scores range from 2 to 4. Only one of the PBFs was nulliparous in 2011, but gave birth in 2012. The rest displayed a mean nipple length of 4.9 mm ± 0.9 *SD* and were parous (nipple length ≥ 4.0 mm). A quarter of these female cases (3 of 12) had only one available male mate, 50% of them had two available mates (6 of 12), and 25% had three available mates (3 of 12). Only 17% (2 of 12) of these females shared breeding with another secondary breeding female. Only in 4 of 12 captures did we observe offspring born to these females. In only one case did we observe two breeding females share the primary mating position in their group (F41 and F42), but only one of them successfully bred and no evidence of an unsuccessful breeding attempt by the other female was observed.

We observed only two identifiable secondary breeding females, with a mean vulvar index of 23 mm ± 3 *SD* and a mean suprapubic gland area of 150 mm ± 23 *SD* (Table VI. 9). One was

nulliparous, and the other is missing a nipple length measurement and so parity remains unknown.

VI. 3. 6. 4: Male *Saguinus imperator*

We assessed 11 primary breeding males (PBM) over 17 capture instances during this study (Table VI. 10). They displayed a mean testicular volume of 890 mm^3 ± 97 *SD* and mean suprapubic gland areas of 96 mm^2 ± 73 *SD*. Their scrotal and suprapubic gland scores ranged from 2 to 5, showing a large range of development and pigmentation. Five males (27%) had two available female mates, while the rest had access only to a single breeding female. Only in 4 cases were males observed mating, and they only mated with the single available breeding female.

We observed 6 secondary breeding males over 7 instances of capture (Table VI. 11). They averaged a mean testicular volume of 635 mm^3 ± 44 *SD* and mean suprapubic gland areas of 34 mm^2 ± 31 *SD*. Only one male was observed mating with a female, but she was an infertile infant that year and the attempt was unsuccessful, and likely a mistake. In three (43%) of the instances, males shared their mates with two other breeding males, while the rest only shared females with one other breeding male. Only two (29%) of the males had two breeding females available to mate with, as most groups only had a single primary breeding female (Table VI. 11).

Primary breeding males shared their mates with two other breeding males in 24% of the cases (4 of 17), with one other breeding male in 59% of the cases (10 of 17) and with no other males in only 17% (3 of 17) of the cases (Table VI. 10). In 4 two-male groups, the average testicular volume of the PBM was 50% ± 24 *SD* greater than that of the SBM (range: 24 – 80 % different). If an additional group with three males (one PBM, two SBMs) is added to the analysis, this difference is maintained (54%± 23 *SD*). In two groups, all males were PBMs and the mean difference between their testicular volumes is 15%± 4 *SD*.

VI. 3. 7: Breeding Status, Mating Systems, and Reproductive Success

We analyzed the group compositions for 15 group-years for *Saguinus fuscicollis* and 12 group-years for *S. imperator* (Tables VI. 12 and VI. 13). We found that two thirds of all cases of *S. fuscicollis* had a single primary breeding female, as compared to 83% of cases of *S. imperator*. We found two monogamous groups of *S. fuscicollis* (13%), and only one produced offspring that year. Similarly, we found three monogamous groups of *S. imperator* (25%), none of which produced offspring. However, other groups were also unsuccessful at producing offspring; among *S. imperator*: SI3 in 2011, with a single PBF and 3 BMs, SI3 in 2012, with the same composition but different actual membership, as well as SI6 in 2011, with 2 breeding females and 2 breeding males, and among *S. fuscicollis*: SF4 in 2010, with 1 PBF, 3 BMs, and 2 nonbreeding but adult females.

In general, only 13% of all cases of *S. fuscicollis* had a single breeding male, with 40% having two breeding males and the remaining 47% with three breeding males (Table VI. 12). In the case of *S. imperator*, 25 % of the groups had a single breeding male, with 50% with two breeding males and the remaining 25% with three breeding males (Table VI. 13). All 8 groups of *S. fuscicollis* that raised twin offspring successfully to 4 mo of age had at least two breeding males. All but one group (of 4) that successfully raised singleton offspring also had at least two breeding males (the exception is a monogamous group). Similarly, all 7 groups of *S. imperator* that raised twin offspring successfully had at least two breeding males, and none of the groups only raised a singleton.

VI. 3. 7. 1: Breeding Behavior Case Studies

Focal groups in each species are described below, for an individual-based analysis of reproductive measures and mating behavior.

Case 1 - Group SF1

Group SF1 was sampled across three years, and used a mating strategy of polygynandry when possible. SF1 produced two sets of infants in all, by different females. F11 had twins in November 2009 but F10 allonursed them (see Section VI. 3. 4; Fig. VI. 2). In 2011, F10 was presumed dead, and Group SF1 had no surviving offspring, one surviving male (M10), and two young adult females in addition to F11. In 2012, F11 then became the PBF, and F13 (daughter from 2009) became the SBF. In 2012, both females mated successfully more often with one male (M12) over the other (Fig. VI. 2).

During their tenures as primary breeding females, F10 and F11 were both in the adult age class; however, F10 transitioned into the older adult class after allonursing, and had higher reproductive values and weight than F11 (Table VI. 14). F13, as an SBF in 2012, had higher reproductive values than F11 did while a PBF. In 2010, M10 became the sole male in the group for two years, after two other adult males disappeared from the group in January. When he was in the presence of the original males in the group, as well as shortly after assuming primary breeding male status, his testicular volume was twice that of what it would become 2011, close to his own displacement by newer males. Overall, his suprapubic gland score increased to 5, appearing more pigmented but maintaining gland area (Table VI. 14). Further, his canines were almost 1 mm shorter on average in 2011, just before his disappearance.

Table VI. 12: Breeding status of all individuals in groups of *Saguinus fuscicollis* throughout the study

Group	Year	PBF	PBM	SBF	SBM	NFF	NFM	Infants	Group Size	Mating System	Demographic events
SF1	1	F10 F11	M10 M11 M12					F12 F13	7	Polyandry	Both females nursed infants
	2	F11	M10			F12 F13		NONE	4	Monogamy	
	3	F11	M13 M14	F13				F14 F15	6	Polygynandry	
SF2	1	F21	M21	F20	M20			NONE	4	Polygynandry	*Friaje* kills F21 and F20
	2	F22	M20 M21					F23 F24	5	Polyandry	F22 immigrated successfully and became the primary breeding female
	3	F22	M20 M21			F23		M22	5	Polyandry	
SF3	1	F31	M30 M31			F30		M32 M33	6	Polyandry	*Friaje* kills all group members
SF4	1	F41	M40 M41		M42	F40 F42		NONE	6	Polyandry	
	2	F41	M40 M41		M42			M43 F43	6	Polyandry	
	3	F41	M41 M42	F43	M43			M44 M45	7	Polygynandry	
SF5	1	F50 F51	M52		M50			M51	5	Polygynandry	Multiple primary females, unable to identify the mother
	2*	F50 F51	M52		M50 M51			F52 F54	7	Polygynandry	
	3	F50 F51	M50 M51 M52			F52 F54		F53	8	Polygynandry	

Table VI. 12 : ***Continued***

Group	Year	PBF	PBM	SBF	SBM	NFF	NFM	Infants	Group Size	Mating System	Demographic events
SF6	3	F61	M60					F60	3	Monogamy	
SF7	3	F70 F71	M70 M73 M74	F72				M71 M72	8	Polygynandry	
Loners	1			LF1					1	Nonbreeding	Roamed briefly with F30
	1				LM1				1	Nonbreeding	
	2			F30					1	Nonbreeding	Roaming alone
	3			F30 LF2					2	Nonbreeding	Relatively stable bachelorette group

Year 1 = 2010; Year 2 = 2011; Year 3 = 2012

PBF = Primary Breeding Female; PBM = Primary Breeding Male; SBF = Secondary Breeding Female; SBM = Secondary Breeding Male; NFF = Non-Fertile Female (usually a young adult); NFM = Non-Fertile Male (usually a young adult); Infants = born in that year, unless otherwise noted, and definitely nonbreeding and infertile.

Mating System: determined based on the number of available reproductively active males and females.

Table VI. 13: Breeding status of all individuals in groups of *Saguinus imperator* throughout the study

Group	Year	PBF	PBM	SBF	SBM	NFF	NFM	Infants	Group Size	Mating System	Demographic events
SI1	1	F10	M11				M10	NONE	3	Monogamy	
	2	F10	M50		M10			M12, M13	5	Polyandry	M50 immigrated into the group
SI2	1	F20	M21		M20, M22			M23, F21	6	Polyandry	
	2	F20	M20		M22	F21		F22 F23	6	Polyandry	
SI3	1	F30	M31 M30		M32*			NONE	4	Polyandry	M32 not trapped but likely breeding as he did the next year
	2	F30	M32 M61 M30					F32, M33	5	Polyandry	F32 and M33 immigrate into SI3 with M61, not born there.
SI4	1	F41 F42	M40		M41			F40, F43	6	Polygynandry	Two indistinguishable primary breeding females
	2	F42	M40 /M41			F43		NONE	3	Monogamy	M40/41 not trapped, but partial collar implies male from year 1
SI5	1	F50	M50 M51	F51				F52 F53	6	Polygynandry	
	2	F50	M51			F52		NONE	3	Monogamy	F52 died post trapping
SI6	1	F60	M60	F61	M61			NONE	4	Polygynandry	F61 dispersed in August
	2		M60 M61					F32 M33	4	Polyandry then non-breeding	F60 gives birth to twins and then dies. M60 and M61 both disperse into SI3, M61 is successful, M60 is displaced and disappears
Loners	1			LF1					1	Nonbreeding	Nulliparous, sub-fertile lone female
	2			F51 UN					2	Nonbreeding	Unknown female roaming with F51, both likely fertile but nulliparous

* Not trapped, so this is an estimated breeding status

Year 1 = 2011; Year 2 = 2012

PBF = Primary Breeding Female; PBM = Primary Breeding Male; SBF = Secondary Breeding Female; SBM = Secondary Breeding Male; NFF = Non-Fertile Female (usually a young adult); NFM = Non-Fertile Male (usually a young adult); Infants = born in that year, unless otherwise noted, and definitely nonbreeding and infertile.

Mating System: determined based on the number of available reproductively active males and females.

Note: Group SI6 in year 2 had a primary breeding female who gave birth to infants and then likely died. Therefore the group was originally polyandrous, but later in the year became nonbreeding and subsequently splintered.

Case 2: Group SI3

Group SI3 was a focal group in 2012. It contained a single female (F30) with three males (M32, M30 and M61) that vied for her attention in July and August 2012. She was observed mating with only M32 and M61 (a recent immigrant), but M30 was capable of breeding (it was a PBM in 2011) (Table VI. 14). Once she mated with M33, unusually, who was an infant class immigrant male born in 2012. Mating success was roughly equal between M32 and M61 (Fig. VI. 2). In 2012, M32 and M61 had similar reproductive characteristics, except M32 (older adult male) had no suprapubic gland development while M61 (the younger male) did (Table VI. 14). In 2011, much less active competition was witnessed between the same males for the two females in the group, and the single breeding male (M30) displayed a small testicular volume. Scrotal scores did not correlate with age (see Chapter V) and were not considered. The PBF was the same for both years, and displayed similar reproductive features with a moderate increase in suprapubic gland area in 2012 (Table VI. 14).

Table VI. 14: Reproductive characteristics of all breeding males and females in both focal groups SF1 and SI3.

Grp.	Individual	Sex	Year	Status	Age-class (Months)	Vulva Sc./ Vulva Index (mm)	Scrotal Sc./ Testicular vol. (mm^3)	Suprapubic gland score/ Area (mm^2)	Nipple length (mm)/ parity
SF1	F10	F	2009	PBF	Ad	4 / 24.4		6 / 606	3.5 / Y
SF1	F11	F		PBF	Ad	3 / Unk.		5 / Unk.	Unk.
SF1	M10	M		PBM	Ad		3 / Unk.	4 / 1509	
SF1	M11	M		PBM	OAd		5 / 443	4 / Unk.	
SF1	M12	M		PBM	Ad		5/ 994	4/ Unk.	
SF1	F10	F	2010	PBF	OAd	4 / 19.8		6 / 226	3.9 / Y
SF1	F11	F		PBF	Ad	3 / 19.6		5 / 133	3.7 / Y
SF1	M10	M		PBM	Ad		3 / 1458	5 / 132	
SF1	F11	F	2011	PBF	Ad*	*		*	*
SF1	M10	M		PBM	Ad		3 / 761	5 / 135	
SF1	F11	F	2012	PBF	Ad	3 / 18.8		5 / 157	4 / Y
SF1	F13	F		SBF	Ad (31)	4 / 21.5		6 / 196	0 / N
SF1	M14	M		PBM	Ad		4 / 1325	4 / 120	
SF1	M13	M		PBM	Ad		3 / 1241	5 / 177	
SI3	F30	F	2011	PBF	OAd	3 / 31.7		3 / 254	5 / Y
SI3	M30	M		PBM	Ad		3/ 753	2/ 0	
SI3	M31	M		PBM	Ad		2 / 417	4 / 143	
SI3	M32	M		SBM	*	*	*	*	
SI3	F30	F	2012	PBF	OAd	3 / 32.7		3 / 345	4.9 / Y
SI3	M32	M		PBM	OAd		5 / 765	2 / 0	
SI3	M61	M		PBM	Ad		5 / 874	2 / 144	
SI3	M30	M		PBM	OAd		3 / 510	2 / 124	

PBF = Primary Breeding Female; SBF = Secondary Breeding Female; PBM = Primary Breeding Male; SBM = Secondary Breeding Male; Y = Yes; N = No; Unk. = Unknown or not recorded; OAd = Older Adult age class; Ad = Adult age class; SF1 = Group 1, *Saguinus fuscicollis*; SI3 = Group 3, *Saguinus imperator*

Grp. = Group Name; Vulva Sc. = Vulva Key Score; Scrotal Sc. = Scrotal Key Score; Testicular vol. = Testicular Volume

Parity = Yes if nipple length ≥ 3.0 mm for *Saguinus fuscicollis* (Soini & Cóppula 1981) and if nipple length ≥ 4.0 mm for *Saguinus imperator*.

* Measurements not taken because animal was not trapped or measurement omitted due to time constraints

VI. 3. 8: Evidence for Reproductive Suppression

Adult or young adult males were observed to be 'nonbreeding' (defined in VI. 3. 5) in none of the 15 groups of *S. fuscicollis* and in only one group of 12 groups of *S. imperator*. Nonbreeding young adult females were found in one third of the groups of *S. fuscicollis* (a total of 8 individuals), and in 25% of the groups of *S. imperator* (3 individuals). All of the nonbreeding females were natal females among *S. imperator*, while two thirds were nonbreeding and natal for *S. fuscicollis*.

In four of the five groups of *S. imperator* we followed for two years, the PBF in year one held her position for both years. The fifth group splintered after the PBF disappeared. Of four groups of *S. fuscicollis* followed for three years, two groups had a single PBF that retained her position for three years, one group had a new PBF who then remained for two years, and one group had two PBFs that shared the position for three years.

VI. 3. 8. 1: Coming of Age in *Saguinus fuscicollis*

A female of Group SF1 born in 2009 achieved SBF status by 2012 (3 y), when new likely unrelated immigrants replaced all the males. In Group SF4, female F43 achieved SBF status in only two years, but with the three same males in her group from the year she was born, of whom one is likely her father. An SBM (M20) achieved PBM status in one year, and retained it for at least one further year. Two males, M42 and M51, remained SBMs for two years before becoming PBMs. Two infants (M43 and M51) achieved SBM status in one year, and one (M51) became a PBM in the next year (i.e. 2 y to PBM). M43 had the reproductive characteristics of a BM, but was not expected to breed in this group because the available females are likely his mother and sister. M51 could breed in the group because it had two PBFs, one that is likely unrelated to him.

Among twin female siblings, two out of three times (F13, F23) only a single female remained in her natal group to achieve SBF status. In the sole bisexual twin pair, both infants

remained in their natal groups till they achieved SB status. All-male twin pairs have not yet been observed for multiple years to determine their fate in their natal groups long-term.

VI. 3. 8. 2: Coming of Age in *Saguinus imperator*

In two cases of twin female siblings (F43 and F52), one sibling each took one year to become a nonbreeding adult, and the other sibling disappeared and was presumed dead. In the case of a bisexual twin pair, the female (F21) became a nonbreeding adult, while the male (M23) disappeared and is presumed dead. No data are available for more than two years.

In Group SI2, the loss of the PBM (M21) caused a SBM (M20) to take its place. In Group SI3, one PBM was lost and a SBM (M32), as well as a recent immigrant (M61), became PBMs. Only one SBM retained its breeding status for two years in a row, and none of the SBFs remained in groups under the same breeding status the second year. In Groups SI5 and SI6, the PBFs retained their breeding status in the second year, and the SBFs each dispersed.

VI. 4: Discussion

VI. 4. 1: Twinning and Birth Statistics

Patterns of extremely high dizygotic twinning among callitrichids were visible in captive conditions (Wislocki 1939; Wislocki 1932). Exact birth rates are unavailable at this site, but our data reveals rates of infant survival up to 4 - 6 mo. We see that all groups successfully raised twins to this age among *Saguinus imperator* while *S. fuscicollis* often raised just singletons at this site. This could be either due to loss of infants among *S. fuscicollis* or due to lower twinning birth rates. Although the present data cannot distinguish between these two outcomes, genetic data collected on singletons could indicate the presence of a deceased sibling if genetic chimerism occurred between them (Hershkovitz 1977b). Rates of chimerism, or the exchange of cells between siblings while in the womb, are as high as 72% (of 36 twin pairs) among twin offspring of *Callithrix kuhlii* (Ross et al. 2007), and chimerism is strongly suspected to be

ubiquitous among all twinning callitrichids (Haig 1999; Heymann 2000b; Wislocki 1939; Wislocki 1932).

Up to four infants have been born at once (multizygotic quadruplets) to marmosets in captivity, largely due to higher quality and consistent nutrition that elevates maternal weights; triplets among marmosets are more common than in tamarins in captivity (Tardif et al. 2003). Our study is consistent with reports from wild *S. fuscicollis* at Cocha Cashu that triplets were never observed, and twins are commonly observed, although exact rates of twinning or twin vs. singleton survival were not specified (Goldizen et al. 1996).

Strong birth seasonality was observed in this study for both species, facilitated by dental records used to identify ages of infants for whom the birth month was not known by observation. Goldizen et al. (1988) observed a later and narrower birth peak for *S. fuscicollis* (November – January as opposed to August – February at CICRA) in which three-quarters of all births occurred, but periods without any births coincide in both populations, occurring during the dry season. The birth season for *S. imperator* observed at this site (November to March) is slightly less wide than that of its close relative, *S. mystax*, observed by Löttker et al. (2004b) (September to May, peaking from November to February) in Northern Perú. *Saguinus imperator* at CICRA and *S. mystax* in northern Perú (Löttker et al. 2004a) share a similarly delayed birth season with respect to either population of *S. fuscicollis* at CICRA or Cocha Cashu (Goldizen et al. 1996).

Overall, these variations could be due to the more seasonal climate in southeast Perú as compared to northern Perú (Heymann 2000c), or more precise ageing of infants in the present study. Alternatively, the broader birth season for *S. fuscicollis* could be due to the higher incidence in this species of multiple females holding primary breeding positions in a group, resulting in even an instance of two females breeding in the same season, several months apart (Group SF7).

The reproductive output of groups is based on infant survival to 4 – 6 mo of age and not birth rates. Due to possible infant mortality from birth to 4 mo of age, reproductive output estimates at this site are an underestimation of true values. Mean reproductive output of *S. fuscicollis* was found to be 1.14 infants per primary breeding female over 13 years of study at Cocha Cashu, slightly lower than the minimum estimated for the same species in this study (1.3 infants per PBF). Further, assuming similar rates of early infant mortality between the two species at this site, *S. imperator* seemed to produce 15% fewer offspring per breeding female than *S. fuscicollis*; unfortunately, mean reproductive outputs per breeding female have not been published for *S. mystax* to afford a comparison. One possible explanation for the lower number of offspring in *S. imperator* is their possibly higher rate of twinning, which places a larger stress on the caretakers in the group. However, both species in the present study exhibit infant survivorship of 89% to at least one year of age, which is higher than that observed in *S. mystax* (maximum of 70.8%) (Löttker et al. 2004a) and on par with estimated survivorship for the Cocha Cashu population of *S. fuscicollis* (*ca*. 85%) (Goldizen et al. 1996). Alternatively, the population of *S. fuscicollis* at this site could be more stable, and it is even possible that groups of *S. imperator* were more negatively impacted by the *friaje* and are as yet recovering. Overall, *S. imperator* appears to be more similar in terms infant survivorship and mean reproductive output to both the CICRA and Cocha Cashu populations of *S. fuscicollis*, than it is to *S. mystax* at other long-term study sites.

Given that these values are minimal estimates of survivorship and do not include mortality from birth to 4 mo of age, it is evident that infant survivorship is higher at this site than others. This could be explained by the scarcity of large-bodied primates at CICRA, a product of previous hunting (see Chapter II) a few decades in the past, suggesting this site sustains infants into adulthood better. Overall density estimates for *S. fuscicollis* at CICRA are *ca*. 18 individuals per km^2, while that of Cocha Cashu is only 10.8 individuals per km^2 (Freese et

al. 1982). Predation at this site has not been comprehensively evaluated; the site does contain a full complement of felid and avian species found commonly in the area, however, their densities have not been assessed (Pitman 2008).

No single pairs have ever been observed to raise twin offspring during the 13-year study period of *S. fuscicollis* at Cocha Cashu, and this is well supported by the present study. A single instance of an unhabituated pair of adult *S. fuscicollis* with twin offspring was observed briefly in 2010, but no evidence on the survival of these infants could be subsequently collected, as they were not included in the capture program. Rates of infant carrying and care can be used to compare the study population to closely related callitrichids at other sites within Perú, and these studies are the focus of future work at this site.

VI. 4. 2: Reproductive Suppression and Breeding Status

We found that both sexes in either species could be allocated primary, secondary or non-breeding status based on measurements of genitalia and suprapubic glands. In general, these measures were consistently more useful in determining capability for breeding than were the morphometric scores based on the visual appearance of anatomy; however, in some cases, such as with female *Saguinus fuscicollis*, morphometric scores proved to be dependable for breeding status determinations. It is possible that while absolute size is related to breeding capabilities, pigmentation and appearance might be subject to seasonal changes or be just individual variation. We also determined that the significantly higher body size of *Saguinus imperator* in comparison to *S. fuscicollis* (see Chapter V) creates corresponding increases in morphometric cutoffs that determine primary breeding status or parity in this species.

VI. 4. 2. 1: Suppression Among Males

An analysis of testicular volumes among *S. mystax* at two sites in northern Peru indicated that in two-male groups, there tends to be one male with considerably larger testicular volumes than the other (from 21 – 152% larger) (Garber et al. 1996). We were able to confirm for *S. imperator* that there is a difference in testicular volumes between primary and secondary breeding males in two-male groups, although the range of absolute variation is smaller with *S. imperator* than *S. mystax* at the sites above. Among *S. fuscicollis* we observed that two-male groups with two primary breeding males showed very little difference between testicular volumes, but those with one primary breeding male and one secondary breeding male showed a very large difference in measurements; this is greater than three times the differences observed among *S. imperator* at this site and *S. mystax* at the two external sites (Garber et al. 1996). Three-male group testicular differences were comparable to similar sized groups in *S. imperator*, and both species at this site showed more differences among males than did three-male groups of *S. mystax*.

Testicular volumes of *Saguinus fuscicollis* appear to have a greater range of variation between primary and secondary males in the same group, than is found in either of the other species considered. Testicle size has been correlated to increased gonadal function in many species, and Garber (1996) has postulated that in the absence of overt aggression or competition between males for females, that subtle nonaggressive competition in the form of hormonal suppression of reproductive capabilities might extend to males in *S. mystax*. Evidence exists of low reproductive behavior among male *Callithrix jacchus* housed within their natal groups (Baker et al. 1999), which can be altered by moving them out of their natal group and into association with an adult female (French et al. 1984). Therefore the differences between the testicular volumes of primary and secondary breeding males, and some times, primary breeding males in groups of > 2 males, could suggest the hormonal suppression of these individuals and reduced reproductive output. From the point of view of behavior, we would require intensive monitoring to judge if sexual behaviors themselves are reduced in such males. A better test would be of hormonal profiles of these males to examine their capability for sperm production, as well as tests of paternity to determine actual reproductive success, especially given that multiple paternity of a single pair of twins is possible among callitrichids (Löttker et al. 2004a). Data thus far suggest that *S. imperator* show stricter suppression of testicular volumes among secondary breeding males, while more variability is observed, especially among larger groups, with *S. fuscicollis*.

Two infant male *Saguinus fuscicollis* acquired secondary breeding status between one and one and a half years of age, and one of them did so despite the two females in his group being his sibling and likely mother. This implies that having unrelated females is not necessary for the acquisition of the morphological characteristics required to breed. The other male also had his mother present, but his group had a second primary breeding female not related to him, which gave him access to an unrelated female. We would predict the likely dispersal of the first

male, should nothing change in his group, and no necessary transfer by the second male. A further analysis of dispersal in this population is presented in Chapter VII.

VI. 4. 2. 2: Suppression Among Females

Despite strong evidence from captive studies for reproductive suppression of subdominant females by the primary breeding females in groups (Ginther et al. 2002; Ziegler et al. 1987), multiple breeding females have been observed in wild callitrichid groups (see Smith et al. 2001 for a review), and in some cases, no differences have been observed between the hormonal profiles of dominant and subdominant females in the wild (*S. mystax*: Löttker et al. 2004b). We observed multiple breeding females in a single group among *Saguinus fuscicollis* (Group SF1 in 2011, Group SF7 in 2012, and Group SF5 in 2010-2012), as were observed in Cocha Cashu (Goldizen et al. 1996), and only once among *S. imperator* at this site (Group SI4 in 2011). This suggests that these groups could have breeding systems that are also polygynandrous, and not merely functionally polyandrous as previously thought (Goldizen 1987a; Sussman & Garber 1987), and this theory will be addressed in Chapter VII.

Although hormonal profiles are being developed for select groups in the present study population, in their absence, we examined genitalia and scent-gland development in conjunction with reproductive behavior to assess sexual maturity in both species. All infertile females, identified as such because of reduced reproductive measures and morphometric scores, are most likely females born into groups in the year before capture. Among *S. fuscicollis,* in groups with multiple female siblings, only a single female typically attained secondary breeding status, with her mother being the primary breeding female in the group; in the case of bisexual twin pairs, both the female and male could acquire secondary breeding status. The suppression of reproduction in these females was minimized when new males entered the groups, or if non-paternal males were already present in the group. In captivity, new males have been shown to cause cycling in a female when removed from her natal group (Epple & Katz 1984; Ziegler et al.

1987), and in the wild, studies have found evidence of suppression in *Leontopithecus rosalia* (French et al. 2003) but not in *S. mystax* (Löttker et al. 2004b); final conclusions on puberty are contingent on endocrine profiling (in progress). However, it appears to take females close to three years since birth to acquire breeding status, so it is possible that suppression is mediated by age.

Moreover, one 20-mo old female *S. fuscicollis* acquired secondary breeding status in her natal group, implying that others that take longer to do so are undergoing some form of reproductive suppression. Given only two years of data on *S. imperator*, it is more difficult to observe these patterns since infants born during the study still remain within their natal groups in most cases. However, we observed that secondary breeding females did not remain within groups for longer than a year, perhaps dispersing because primary breeding females retained their positions for both years in most cases. Final conclusions on reproductive suppression will depend on correlating endocrine profiles with morphology and behavior (Huck et al. 2004b), which is currently being undertaken at this site.

VI. 4. 3: Breeding Strategies

Since the turnover of primary breeding females in both species was extremely low, it appears that breeding vacancies are extremely hard to come by, as was observed to be the case at Cocha Cashu (Goldizen et al. 1996) and Padre Isla (Garber et al. 1993). Garber observed that with *S. mystax,* females are more likely to find open breeding positions if they disperse than if they stay in natal groups (Garber et al. 1993); at this time, we have several young females poised in secondary breeding positions in their natal groups and with further study we may determine how long they need to remain there to be successful at breeding on their own. The advantages and risks to dispersing females are discussed in Chapter VII.

While it took natal females at least two years to acquire secondary breeding status within groups, young males displayed morphological features developed enough for breeding in their

second year of life, acquiring secondary breeding status quicker; they were especially successful in groups with multiple primary breeding females, where mating opportunities were available with a fertile female that was not their mother. These factors confirm that in both species, and possibly to a greater extent in *Saguinus imperator*, which expressed lower turnover of primary breeding females, male and female breeding strategies differ significantly, with more reproductive opportunities available to males than females. Data from *S. fuscicollis* (Goldizen et al. 1996) and *S. mystax* (Garber et al. 1993) confirm these factors, and the role that dispersal plays in providing further breeding opportunities to males will be discussed shortly in Chapter VII.

Given the propensity in both species for multiple males in each group, which is in turn strongly conducive to the successful raising of infants, seen here and in other studies (Garber 1997; Sussman & Garber 1987), polyandry and polygynandry are the most common mating systems observed by callitrichids both at this site and others (Garber et al. 1993; Goldizen 1987b; Huck et al. 2004a; Terborgh & Goldizen 1985). Males typically have at least some access to the primary breeding female, although mate-guarding behaviors were observed in *S. imperator* at this site, but the final determination of paternity could be dependent on a variety of factors including the number of mating opportunities, mating opportunities during particular times of the year (likely correlating with peak conception periods), as well as the physiological capability of individual males.

VI. 4. 4: Lactation and Mating

Our focal group of *S. fuscicollis* had two primary breeding females, one of which gave birth and both of which nursed the same pair of offspring. Nursing periods lasted from 3.6 – 4.2 months, with anything from 30 to 50 days at the end involving weaning behaviors. We observed a strong correlation between low mating rates during nursing periods (0.4 – 12. events per month), and weaning behavior coincided with increased rates of mating (4 – 4.8 events per

month). The allonursing was likely due to an unsuccessful pregnancy during which the female mated at a low rate (1.9 events per month). In contrast, mating frequency increased rapidly post-weaning, and ranged from 2.4 events per month (March to August), to as high as 11 events per month in August alone. Several instances of species with multiple breeding females have been observed in the wild (cf Smith et al. 2001), but allonursing was only observed among *Callithrix jacchus* and *Callithrix flaviceps* in wild populations. Based on the review by Smith et al. (Smith et al. 2001), *S. fuscicollis* (including the population at Cocha Cashu), *S. oedipus* and *S. mystax* show evidence of multiple breeding females but never allonursing. At CICRA, we have evidence among *S. fuscicollis* for multiple primary breeding females in three groups over 5 years and for one group of *S. imperator* in a single year. It appears that breeding strategies among *S. fuscicollis* are more flexible, with the distinct possibility that imperfect hormonal suppression occurs in some cases.

VI. 4. 5: Final Thoughts

In conclusion, the current population of sympatric callitrichids at CICRA displays many of the same reproductive trends documented for both sexes at other sites. However, this study provides additional information related to development and sexual maturation that allow a broader perspective on reproductive trends. Evaluation of morphology, focusing on both the external appearance and size of genitalia and suprapubic glands, reduces the risk of underestimating the number of individuals capable of breeding. These data are helpful in identifying differences between the two species, and emphasize that universal guidelines for using morphology to determine breeding status (Garber et al. 1996; Soini & Cóppula 1981) are likely to be inaccurate across species of callitrichids. Second, the identities of possible participants in reproduction are known and rarely left to guessing based on behavior, group membership or other demographic variables. Further research on endocrine and genetic profiles of this population will allow us to analyze kinship and relatedness within the population, and overlay the genetic structure to the social and reproductive patterns outlined in this study.

VI. 5: Chapter Summary

1. Twinning and strong birth seasonality were observed in both species, with a narrower birth season witnessed in *Saguinus imperator* than in *S. fuscicollis*.
2. Although we underestimated reproductive output due our inability to assess early infant mortality, we still have values that are higher than that of neighboring Cocha Cashu, likely because of the lack of large-bodied primates at CICRA.
3. Some adult males exhibit lower testicular volumes (more so among *Saguinus imperator*), and future assessments of endocrinology are necessary to test if their testosterone levels are suppressed, indicating reproductive suppression of subdominant males.
4. Reproductive suppression among females is not very strong, particularly among *Saguinus fuscicollis*, with several instances of multiple primary breeding females in a group, as well as multiple breeding in a group observed at this site.
5. Males appear to more rapidly acquire secondary breeding positions, on average one year faster than do females of either species, despite no access to unrelated females.

Chapter VII: Demographic Events in Wild Sympatric Saddleback and Emperor Tamarins (*Saguinus fuscicollis* and *S. imperator*)

VII. 1: Introduction

The flexible social organization of callitrichids across the Amazon basin (Goldizen 1987b; Savage & Baker 1996; Sussman & Garber 1987; Sussman & Kinzey 1984; Terborgh & Goldizen 1985) supports the idea that the natural habitat of the Callitrichidae, fragmented by dozens of rivers, has created an array of adaptations and a likely ability to adapt to changing ecological conditions among these primates (Cropp 1997; Cropp et al. 1999; Díaz-Muñoz 2010; Hershkovitz 1977b). In the majority of studied species, polyandry or polygynandry appear to be the most common mating systems (Garber et al. 1993; Goldizen 1987a; Goldizen 1987b; Huck et al. 2005a; Sussman & Garber 1987; Terborgh & Goldizen 1985), although a single group can exhibit the full range of mating systems throughout its existence (Goldizen et al. 1996). Fertile polygynandrous individuals, i.e. those with the physiological capability to mate, have several choices – the number of mates to have, whether to share them with others of the same sex, as well as which individuals to mate with at any given time (Goldizen et al. 1996). Most individuals in these groups, however, are not offered all choices for a variety of reasons.

Given inbreeding avoidance (Huck et al. 2007) and long tenures of dominant breeding females (Goldizen et al. 1996), the acquisition of a breeding position in a group is dependent on factors such as age, relatedness, group composition, resource availability, and stochastic environmental change likely cause individuals to modify their mate-finding strategies to fit their circumstances (Field & Guatelli-Steinberg 2003; Fiore 2009). Dispersal from their natal group is one of the available choices. One of the most important decisions a callitrichid must make regards their first attempt at acquiring a breeding position in a group is that of when to disperse, if at all, to a new group. Indeed, the outcome of this choice could effectively determine the future success of their lives. These interactions can only be understood by examining the choices made by individual callitrichids and the contexts for those choices in the wild.

The ability to study known individuals has significant impacts on understanding individual mate choices as well as the factors that determine breeding vacancies within groups. To date, field studies of demographic and reproductive variation among tamarins have been largely restricted to group-level investigations (Garber et al. 1984; Porter 2001; Windfelder 1997a), due to inter-individual morphological homogeneity that precludes the reliable identification of individuals within groups. In some cases however, field studies have attempted to identify individuals through identification tags (Garber et al. 1993; Goldizen & Terborgh 1989; Savage et al. 1997; Suárez 2007; Terborgh & Goldizen 1985) or via genetic analyses of fecal samples post-hoc (Huck et al. 2005a). Of these, only a handful have included more than one tamarin species at the same site (Bicca-Marques & Garber 2003; Garber 1988; Garber 1986).

The following study of two sympatric tamarin species, *Saguinus fuscicollis* and *Saguinus imperator,* describes both inter- and intraspecific variation in demographic and reproductive variables across three years in southeastern Perú. Each individual has an assigned age-class based on dental condition (Chapter IV), as well as a known breeding status from morphological variation analyzed in Chapters V and VI. Changes in sex ratios, or the proportion of adults made up by males, will be used to address if sex, seasonality, or both, affect group compositions of either species. Group compositions may change due to births, deaths and dispersal events, although in reality many disappearances of individual tamarins cannot be assigned a determinate cause. Each possible outcome will be analyzed for both species, and age, sex and breeding status of a subset of individuals that were observed to successfully disperse during the study will be examined.

With these data, the following questions will be addressed: What are the determinants for dispersal in either species? Which factors affect the availability of breeding vacancies in either species? Is dispersal a successful strategy for the acquisition of breeding opportunities by avoidance of reproductive suppression within a group? What are other strategies available to

fertile individuals who wish to breed? For each of these questions, we seek not only to identify predominant patterns but also the variability observed in these naturally sympatric tamarins.

VII. 1. 1: Facultative Polyandry

A thirteen-year study of five groups of *Saguinus fuscicollis* at Cocha Cashu in Manu National Park, Peru, suggested the theory of facultative polyandry as the likely mating strategy among groups of this species (Goldizen et al. 1996; Goldizen 1987b). The theory suggests that a) a male-female pair with at least one non-fertile helper (> 1.5 y of age) could breed monogamously and successfully raise twin offspring and b) both the male and female of a lone pair lacking non- fertile helpers would benefit by recruiting other individuals and mating either polyandrously, polygynously or both with them. The theory itself was inferred from and supported by several key pieces of evidence: (1) monogamous pairs without helpers were never observed to raise infants successfully without recruiting help (Goldizen et al. 1996; Goldizen 1987b), (2) older offspring contribute significantly to carrying of infants (Goldizen 1987b), and (3) all new bisexual groups formed during thirteen years of study contained two adult males (Goldizen et al. 1996).

We know that monogamous pairs have shown little to no reproductive success in this study population for either species, and have seen varying degrees of polyandry among groups (*cf* Chapter VI), indicating that these species might adopt facultative polyandry. Several factors allow us to test this theory in this study: 1) Group membership is known for all individuals spanning the study duration, 2) While the fates of all animals that disappeared cannot be verified, we have recorded all successful immigrants and a large number of emigration events, 3) We can assess the effect of dispersal events on group stability and 4) The breeding status of each immigrant is known, allowing for an assessment of their participation in actual or potential mating events. We cannot be certain that all mating events were recorded that occurred during

the study, and so mating systems were based not entirely on observed mating, but the potential for breeding among adults in a group as assessed from morphology (see Chapter VI).

We will use data from this study to formulate answers to the following questions suggested by this theory:

A: Do groups with infants that survive 1.5 y from birth accept new individuals?

- The theory of facultative polyandry suggests that they should choose to mate monogamously, avoid recruiting new helpers, and use their non-fertile infants as helpers instead.

B: If groups with helpers were polyandrous to begin with when the offspring were born, then what are the fates of supernumerary males and females now that nonfertile helpers (i.e. individuals not mature enough to breed for whom this is the natal group) are available?

- The theory does not offer a solution to these situations, but one could expect either the dispersal of these 'extra' individuals, or their reproductive suppression to ensure monogamous mating between the primary breeding pair.

C: Do groups without non-fertile helpers utilize mating systems involving at least more than one member of either sex, i.e. do adults in these groups have available to them multiple potential mates of either sex?

- The theory of facultative polyandry indicates that this should occur because monogamous lone pairs without helpers recruit adults by being polyandrous, polygynous or both.

VII. 2: Methods

VII. 2. 1: Study Population

Over the course of three trapping seasons, we captured and marked 57 *Saguinus fuscicollis* (in 7 groups) and 36 *S. imperator* (in 6 groups). We observed groups of *S. fuscicollis* for 19 non-consecutive months, and for 13 of those months, we also monitored groups of *S. imperator*. Several groups of either species were recaptured across multiple trapping seasons (Table VII. 1). Group compositions were monitored closely across all study months with regular monthly censuses to assess social organization throughout each month of the study. Data are presented in as detailed a manner possible to facilitate comparison to other study sites in the future (Goldizen et al. 1996; Goldizen & Terborgh 1989; Löttker et al. 2004a). The age-composition of the groups was derived from dental records collected during capture (see Chapter IV).

VII. 2. 2: Sex Ratios

VII. 2. 2. 1: Population Level Ratios

We calculated the overall adult sex ratio (# adult males to females) per year for each species and tested if it differed significantly from a 1:1 ratio using a Pearson's chi-square goodness of fit test ($\alpha = 0.05$). We repeated this test for adult sex ratios in the beginning and end of the study (typically April and August) of each year, and used a paired Wilcoxon rank sum test ($\alpha = 0.05$) to see if the sex ratios differed across the year.

VII. 2. 2. 2: Group Level Ratios

First, we calculated the ratio of males to females in each group per month of the study, including both adult and older adult age-classes (SRa).

$$SRa = \frac{\text{\# males (adult or older) in a group}}{\text{\# females (adult or older) in a group}}$$

In instances with single-sex groups, this ratio becomes mathematically redundant, and so sex ratios were also calculated as the proportion of adult individuals in a group that are male (SRb) (Löttker et al. 2004a; Wilson & Hardy 2002).

$$SRb = \frac{\text{\# males (adult or older) in a group}}{\text{\# males + females (adult or older) in a group}}$$

Sex ratios of type SRb were calculated each year for each age class, and then averaged across years to arrive at an age-specific group sex ratio (ASRb) for each species. SRb values < 0.50 indicate more females than males.

We also calculated the average operational sex ratios (OSR) for groups of each species, defined as the number of fertilizable females present per adult sexually active male (Emlen & Oring 1977), as well as the number of primary breeding females per adult sexually active male (Löttker et al. 2004a), to assess the intensity of sexual competition in each species.

VII. 2. 3: Group Composition

Group composition changes could be attributed to the following causes: births, deaths, disappearances, or known emigration or immigration events. We calculated individual persistence, or the proportion of animals present in April who were also present one year later, to determine the overall stability of groups across time. We then examined the circumstances for an individual not to persist across a given year. Birth and breeding statistics from chapter VI were used to identify the effect of breeding status and reproductive output on individuals that disappeared, died, or were observed to emigrate or immigrate. Individuals were presumed dead if they were infants and missing from their natal group within one year of birth, or older adults missing from their groups, as such dispersals were considered to be extremely unlikely to succeed.

Table VII. 1: Trapping instances per group for *Saguinus fuscicollis* and *S. imperator* species across the study period.

	Season I							Season II		Season III	
Group Name	**Nov. 2009**	**Dec. 2009**	**Mar. 2010**	**Apr. 2010**	**May 2010**	**Jun. 2010**	**Jul. 2010**	**Apr. 2011**	**May 2011**	**Jun. 2012**	**Jul. 2012**
SF1	X	X	X	X	X		X	X		X	
SF2			X					X		X	
SF3					X		DEAD*				
SF4					X			X		X	
SF5						X				X	
SF6										X	
SF7											X
SI1								X		X	
SI2								X		X	
SI3								X		X	
SI4								X		X	
SI5									X	X	
SI6									X	X	

SF = *S. fuscicollis*; SI = *S. imperator*

* confirmed death due to recovery of remains

VII. 2. 4: Breeding Status

We identified two classes of breeding for dispersing individuals, defined by reproductive measures from Chapters V and VI as follows:

Infertile Young Adult Females: Young females in their natal group that were not observed to mate and had underdeveloped genitalia and/or scent glands (regardless of dentally determined age).

Roaming Fertile Females: Females outside natal groups, either alone or with other females, that are capable of breeding but have not yet bred successfully. These females have reproductive morphology (genitals and scent glands) of breeding females, but do not have developed nipples and are thus identified as nulliparous.

Infertile Young Adult Males: Young males within their natal groups without primary or secondary breeding status, as determined based on lack of observed mating events and underdeveloped genitals and/or scent glands.

Roaming Fertile Males: Males outside their natal groups that are fertile or display the capability for breeding, either roaming alone or in conjunction with same sex individuals. Successful paternity is indiscernible among males.

Most individual dispersers were captured and evaluated once annually, but this could have occurred just before dispersal, during dispersal, or after a successful migration event.

VII. 2. 5: Dispersing Events

Animals transferred from one group to another under different circumstances. We modified the demographic event descriptions used by Löttker et al. (2004a) to suit this study as follows:

Visit: An animal enters a group for < 1 month but then leaves it and continues to disperse.

Temporary Shift: An animal leaves their group for < 1 mo but returns and is accepted back into it.

Immigration: An animal stays in a group for > 1 month after entry or acquires a breeding position within the new group.

Emigration: An animal leaves its group and is either alone or roaming with other same-sex individuals. Observed emigrations are cases in which the animal is actually observed to make the transition out of the group.

Disappearance: Loss of an animal with its fate unknown. Typically, if it is a young adult or adult, it is presumed to sustain a chance of survival in the area, albeit unbeknownst to our observers. Older adults and infants that disappeared were presumed dead.

Death: An animal is found dead, is observed to disappear after sustaining a visible injury, is an infant or an older adult at the time of its disappearance.

VII. 2. 6: Testing Facultative Polyandry

We identified groups with infertile infants of 1.5 y, i.e. undergoing their second capture since birth, and calculated the proportion of those groups, in both species, that accepted immigrants into breeding positions. For each of these groups, we identified if a monogamous mating was practiced, and if so, what the fates were of the extra breeding individuals, if any, already present in the group. We also noted the reproductive output for these groups, based on survival of infants for 4-6 months. Finally, we identified groups without non-fertile helpers in a given year and classified the flexibility of their mating systems.

VII. 3: Results

During this study, *Saguinus fuscicollis* was observed over 106 group-months, while *S. imperator* was watched for 81 group-months. We found the average group size (recorded in August of each year) of *Saguinus fuscicollis* to be 5.1 individuals (range: 2- 8 animals) and of *S. imperator* to be 4.1 individuals (range: 2 - 7 animals.

VII. 3. 1: Social Structure

Single male-multi female groups (42% of group months) and multi-male, multi-female groups (36 % of group months) are the most common forms of social organization among *Saguinus imperator*. *Saguinus fuscicollis* is primarily organized as multi-male, multi-female

groups (52% of all group months) (Fig. VII. 1). Bachelorette groups were more often observed in *S. fuscicollis*, but only *S. imperator* was observed to have all male groups. This occurred for a few months, when the dominant breeding female died in Group SI 6 (Fig. VII. 1).

VII. 3. 2: Sex Ratios

VII. 3. 2. 1: Population Sex Ratios

The overall ratio of adult males to females was not significantly different from 1:1 in any year of the study, for either species, whether calculated in April or August (Pearson's goodness of fit test, $p > 0.05$). Mean sex ratios for *S. fuscicollis* were 1.6 ± 0.9 SD in April and 1.2 ± 0.1 SD in August and for *S. imperator* they were 1.4 ± 0.5 SD in April and 1.6 ± 0.8 SD in August) (Fig. VII. 2, Tables VII. 2 and VII. 3).

VII. 3. 2. 2: Group Sex Ratios

Both mean group sex ratios, SRa and SRb, were not significantly different from the earliest study month to August at the end of each season (SRa: *S. fuscicollis* 1.30 ± 0.4 SD to 1.51 ± 0.3 SD, *S. imperator* 1.25 ± 0.4 SD to 1.46 ± 0.7 SD; SRb: *S. fuscicollis* 0.53 ± 0.03 SD to 0.56 ± 0.03 SD, *S. imperator* 0.53 ± 0.05 SD to 0.58 ± 0.09 SD) (Wilcoxon paired test, $p > 0.05$) (Fig. VII. 2). There were 0.7 ± 0.3 SD fertile females and only 0.6 ± 0.3 SD primary breeding females available per sexually active male (OSR) among both *S. fuscicollis* (n = 15 group years) and *S. imperator* (n = 12 group years).

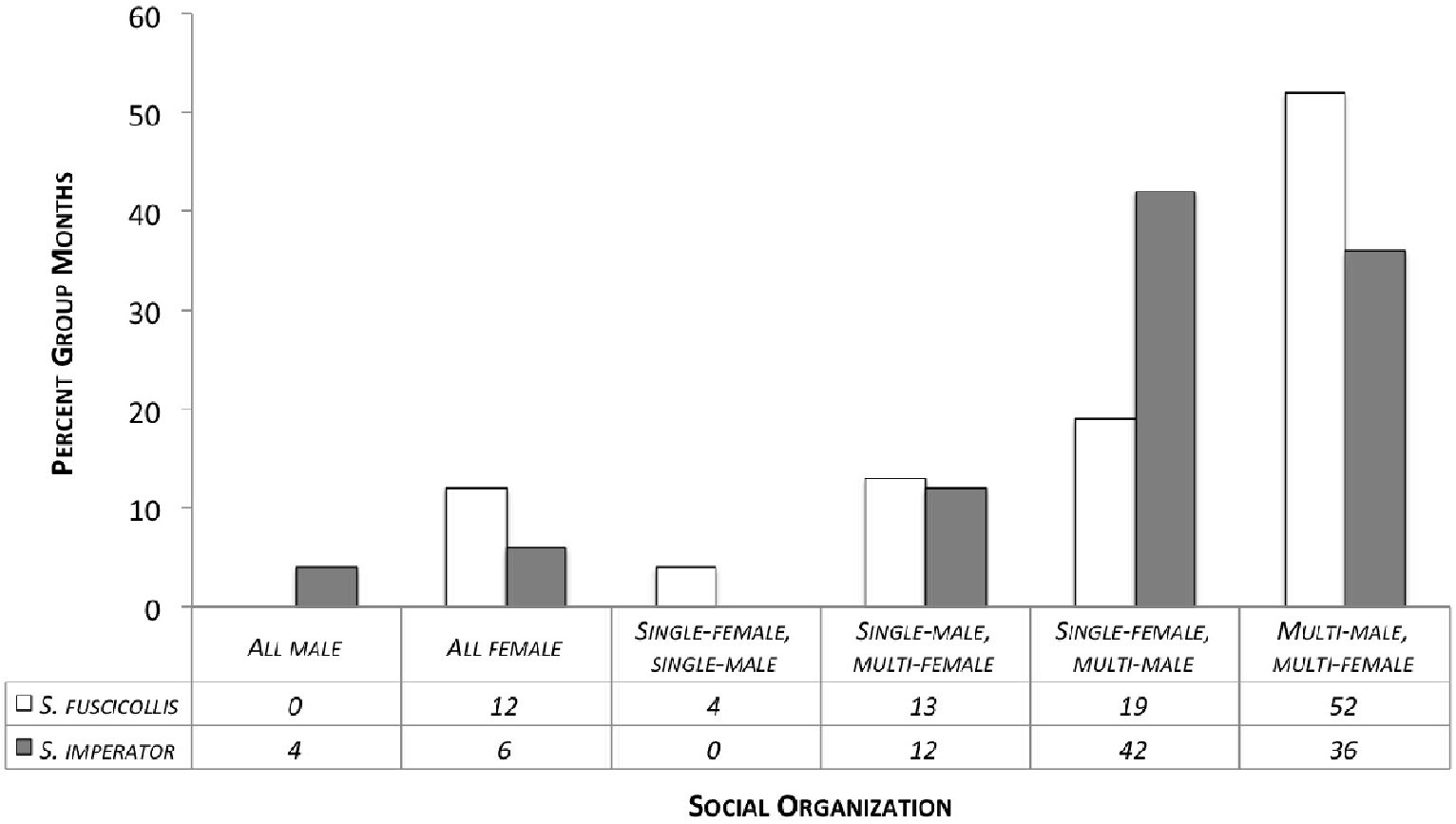


Figure VII. 1: Percent group months in which specific social organization patterns were observed. Total number of group-months included were 106 for Saguinus fuscicollis and 81 for S. imperator. Note that data from group-months are not independent, and are affected by group compositions in preceding months. The time interval of a month was used for convenient censuses and for comparison to previous studies. These groups do not include single dispersing individuals, but do include pairs of dispersing individuals.

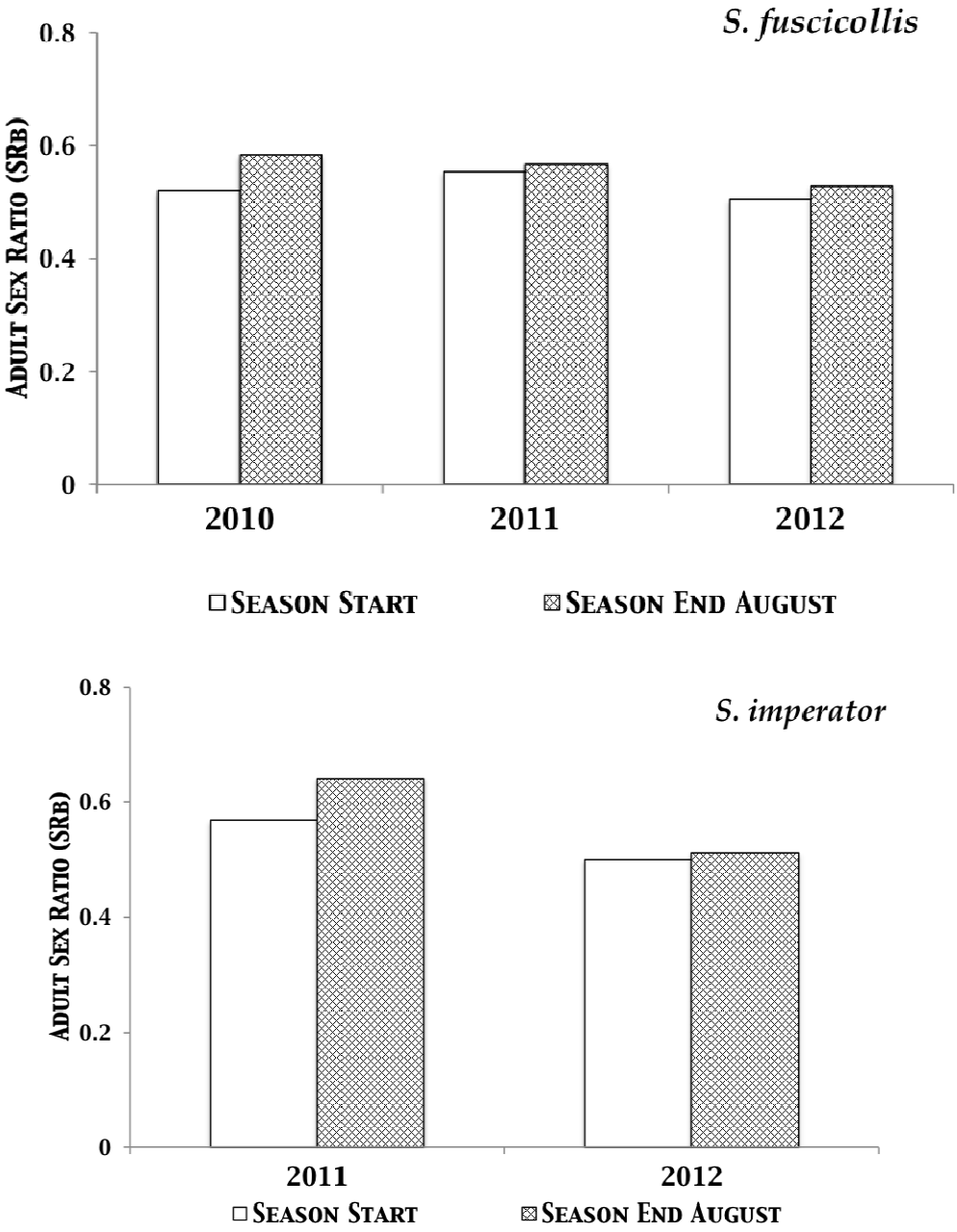


Figure VII. 2: Average sex ratios in the beginning and end of each field season for both species. SRb = the proportion of all adults in each group that are male in a particular month. Similar trends were observed (not shown here) with sex ratios (SRa). No significant differences across the year in either calculation of sex ratios.

VII. 3. 2. 3: Age-Specific Group Sex Ratios

There were no significant differences in sex ratio (ASRb) between the four age-classes among *Saguinus fuscicollis* (Kruskal Wallis test, $p > 0.05$) whether calculated in April ($H = 1.34$, $df = 2$) or August ($H = 5.28$, $df = 2$) of each year. This pattern is likely to hold true among *S. imperator* but more years of data are required to test this idea in the same manner. The expected values within each class are < 5 in most cases, making it impossible to test for sex bias within the populations using a Person's goodness of fit test, for either species. The mean number of individuals of an age-class within a group for each species is provided in Table VII. 4A, and mean age specific sex ratios are detailed in Table VII. 4B.

Table VII. 2: Number of individuals per age-class in each group of *Saguinus fuscicollis* at the earliest and latest months of each year of the study

Group Name		Infants		Young Adults		Adults		Old Adults	
2010		M	F	M	F	M	F	M	F
SF1	Jan		2			2	2	1	
	Ag		2			1	1		1
SF2	Jan					2	2		
	Ag					2	1		
SF3-	Jan	2				1	2	1	
	Ag	-				-	1	-	
SF4	Jan				1	3	2		
	Ag				1	3			
SF5	Jan	1				2	2		
	Ag	1				2	2		
2011									
SF1	Ap					1	3		
	Ag					1	3		
SF2	Ap		2			2	1		
	Ag		2			2	1		
SF4	Ap	1	1			3	1		
	Ag	1	1			3	1		
SF5	Ap		2*			3	2		
	Ag		2*			3	2		

Table VII. 2: ***Continued***

2012									
SF1	Ap		2			2	2		
	Ag		2			2	2		
SF2	Ap	1				2	2		
	Ag	1				2	2		
SF4	Ap	2				3	1		1
	Ag	2				3	1		1
SF5	Ap		1			3	4		
	Ag		1			3	3		
SF6	Ap	1				1	1		
	Ag	1				1	1		
SF7	Ap	1		1		2	2	1	1
	Ag	1		1		2	2	1	1

M=# of males; F=# of females; SF = Saguinus fuscicollis; Ap=April; Ag=August, Jan=January

* Although not trapped this year, based on ageing of teeth from 2012, we determined they were born in 2011. At least 1 other adult was present but not trapped.

Note: SF3 was omitted from 2011 and 2012 because the group perished after the 2010 friaje

Table VII. 3: Number of individuals per age-class in each group of *Saguinus imperator* at the earliest and latest months of each year of the study

Group Name		Infants		Young Adults		Adults		Old Adults	
2011		M	F	M	F	M	F	M	F
SI1	Ap			1	1	1			
	Ag			1	1	1			
SI2	Ap	1	1		1	2		1	
	Ag	1	1		1	1		1	
SI3-	Ap					3			1
	Ag					3			1
SI4	Ap		2			2	2		
	Ag		2			2	2		
SI5a	Ap			1		1	3		
	Ag			1		1	2		
SI6	Ap				1	2	1		
	Ag				1	2			
2012									
SI1	Ap	2				2	1		
	Ag	2				2	1		

Table VII. 3: ***Continued***

Group Name		Infants		Young Adults		Adults		Old Adults	
SI2	Ap		2		1	1	1	1	
	Ag		2		1	1	1	1	
SI3	Ap*					1		2	1
	Ag*			1	1	1		2	1
SI4	Ap					1	2		
	Ag					1	2		
SI5a	Ap					1	3		
	Ag					1	2		
SI5b	Ap						2**		
	Ag						2**		
SI6	Ap	1	1			1			
	Ag	-	-			-			

** age-class had to be estimated because of lack of dental cast for one or more individuals; Ap = April, Ag = August, SI = *Saguinus imperator*, M = Male, F = Female

Table VII. 4A: Average number of individuals per age-class per group of each species.

Species	**Inf** ♀	**Inf** ♂	**YA** ♀	**YA** ♂	**Ad** ♀	**Ad** ♂	**OAd** ♀	**OAd** ♂
S. fuscicollis	0.7	0.5	0.1	0.1	1.5	2.0	0.2	0.1
S. imperator	0.4	0.2	0.4	0.2	0.9	1.2	0.2	0.3

Inf = Infant, YA = Young Adult, Ad = Adult, OAd = Older Adult

Table VII. 4B: Mean age-specific group sex ratios for both species across the study period.

ASRb	**Inf**	**YA**	**Ad**	**OAd**
Saguinus fuscicollis in April	0.46 ± 0.3	0.33 ±0.6	0.44 ± 0.4	0.78 ± 0.4
Saguinus fuscicollis in August	0.37 ± 0.2	0.33± 0.6	0.43 ± 0.1	0.10 ± 0.2
Saguinus imperator in April	0.40 ± 0.1	0.2 ± 0.3	0.50 ± 0.1	0.65 ± 0.2
Saguinus imperator in August	0.40 ± 0.1	0.35 ± 0.1	0.45 ± 0.2	0.63 ± 0.2

Inf = Infant, YA = Young Adult, Ad = Adult, OAd = Older Adult, All = all years;

ASRb: Sex ratio (SRb) calculated for individuals of each age class. Numbers is parentheses indicate values for the end of the field season in August, and others indicate value for the beginning of the field season each year.

VII. 3. 3: Group Composition Changes: Mortality

Changes of group composition occurred due to deaths, dispersals and disappearances across a study period (Tables VII. 5 and VII. 6).

There were 12 cases of suspected mortality among *S. fuscicollis* during three years, and 4 cases among *S. imperator* in two years. Among *S. fuscicollis,* these include 2 male twin infants, 1 female infant, 3 adult females, 2 adult males, 3 older adult males and 1 older adult female. The mortalities among *S. imperator* were of 2 female infants, 1 male infant and 1 young adult female. In three cases, two among *S. fuscicollis* and one *S. imperator*, deaths were observed and confirmed with carcasses. (1) A day after the 6-day long cold-spell or *friaje* in July 2010, the collar and carcass of the dominant breeding female of Group SF3 was found at the base of a popular sleeping tree of this group. Death was due to a possible predator attack, or cold, and none of the group's five inhabitants were ever observed again. (2) A lone male that appeared at the field station in December 2009, was found nearly blind in February 2010, and was confirmed dead in June 2010 when his collar was found intact. We found a large and relatively mobile growth near his scrotum, poor body condition, and worn teeth of an older adult. (3) The death of a young adult *S. imperator* is described elsewhere (see Chapter III).

Table VII. 5A: Changes in group composition of *Saguinus fuscicollis* based on trapped groups alone.

	Group Names:	SF1	SF2	SF3	SF4	SF5
Study Period		January – August 2010 (8 months)				
Group Size	Start	7	4	4	6	4
Number of Adults	Males	3	2	2	3	2
	Females	4	1-2	1-2	3	2
Recruitment	Infants born	+2♀	0	+2♂	0	+1♂
	Immigrations	0	+1♀	0	0	0
Losses	Emigrations	0	0	-1♀	-2♀	0
	Disappearances	-2♂	-2♀	0	0	0
	Deaths	0	0	-5(all)	0	0
Group Size	End	5	3	0	4	5
Group Off-View		September 2010 – February 2011 (6 months)				
Group Size	Start	5	3	-	4	5
Recruitment	Infants born	0	+2♀	-	+2♀,♂	+2♀
	Immigrations	0	0	-	0	0
Losses	Emigrations	0	0	-	0	0
	Disappearances	0	0	-	0	0
Group Size	End	5	6	-	6	7
2011		March – August 2011 (6 months)				
Group Size	Start	5	6	-	6	7
Number of Adults	Males	1	2	-	3	3-4*
	Females	4	1	-	1	2-3*

Table VII. 5A: Continued

	Group Names:		SF1	SF2	SF3	SF4	SF5	
Recruitment	Infants born		0	0	-	0	0	
	Immigrations		0	0	-	0	0	
Losses	Emigrations		0	0	-	0	0	
	Disappearances		-1♀	0	-	0	0	
	Deaths		0	0	-	0	0	
Group Size	End		4	5	-	6	7	
Group Off-View	September 2011 – March 2012 (6 months)							
Group Size	Start	4	5	-	6	7	-	-
Recruitment	Infants born	+2♀	+1♂	-	+2♂	+1♀	+1♀	+2♂**
	Immigrations	+2♂	0	-	0	0	-	-
Losses	Emigrations	-1♀	0	-	0	0	-	-
	Disappearances	-1♂	-1♀	-	-1♂	0	-	-
Group Size	End	6	5	-	7	8	3	8
2012	April – August 2012 (5 months)							
Group Size	Start	6	5	-	7	8	3	8
Number of Adults	Males	2	2	-	3	3	1	3
	Females	2	2	-	2	4	1	3
Recruitment	Infants born	0	0	-	0	0	0	0
	Immigrations	0	0	-	0	0	0	0
Losses	Emigrations	0	0	-	0	-1♀	0	0
	Disappearances	0	0	-	0	0	0	0
	Deaths	0	0	-	0	0	0	0
	End	6	5	-	7	7	3	8

SF = *S. fuscicollis;* SI = *S. imperator*

* This group was not trapped in 2011, and so while group size is known, exact sex composition of the adults is unknown

** Infants born to Group SF5 are not siblings and were born some months apart based on dental eruption.

Table VII. 5B: Changes of group composition of Saguinus imperator based on trapped groups alone.

	Group Names:	SI1	SI2	SI3	SI4	SI5		SI6
2011		January – August 2011 (8 months)						
Group Size	Start	3	4	4	4	6		4
Number of Adults	Males	2	3	2	2	3		2
	Females	1	1	2	2	3		2
Recruitment	Infants born	0	+2♂,♀	0	+2♀	0		0
	Immigrations	0	0	0	0	0		0
Losses	Emigrations	0	0	0	-1♀	-1♀***		-1♀
	Disappearances	0	0	0	0	0		0
	Deaths	0	0	0	0	0		0
	End	3	6	4	5	5		3
Group Off-View		September 2011 – March 2012 (7 months)						
Group Size	Start	3	6	4	5	5		3
Recruitment	Infants born	+2♂	+2♀	0	0	0	0	+2♀,♂
	Immigrations	+1♂*	0	+2 ♂****	0	0	+1♀***	0
Losses	Emigrations	0	0	-2 ♂	0	0	0	-1♂****
	Disappearances	-1♂	-1♂	0	-1♂	-1♂*	0	-1♀
	Deaths	0	-1♂	0	-1♀	0	0	0
Group Size	End	5	6	4	3	2	2	3

Table VII. 5B: Continued

2012		April – August 2012 (5 months)						
	Group Names:	SI1	SI2	SI3	SI4	SI5		SI6
Group Size	Start	5	6	4	3	4	2	3
Number of Adults	Males	3	2	3-5	1	1	0	2
	Females	1	1-2	1-2	2	2-3	2	1
Recruitment	Infants born	0	0	0	0	0	0	0
	Immigrations	0	+1♀**	+5 (4♂, 1♀)*****	0	0	0	0
Losses	Emigrations	0	-1♀**	-1♂	0	0	0	-3(2♂, 1♀) *****
	Disappearances	0	0	0	0	0	0	0
	Deaths	0	0	-1♀	0	-1♀	0	0
	End	5	6	6	3	3	2	0

SF = *S. fuscicollis;* SI = *S. imperator*; * immigrant from SI5; ** the same female left SI2 for SI3 briefly, and then returned to natal group SI2; *** this female dispersed in 2011, but then returned to her original group; **** one male from SI6 immigrated into SI3; ***** all three dispersed to SI3, includes a pair of twins of both sexes.

Table VII. 6: Summary of changes in group-composition recorded during the entire study

	Saguinus fuscicollis	*Saguinus imperator*
Study Period (mo)*	19	13
Number of litters	11	5
Number of infants	20 (9 ♂ & 11 ♀)	10 (4 ♂, 6 ♀)
Adult Immigrations	3 (2 ♂, 1 ♀)	3 ♂
Known deaths	7 (6 ♂, 1 ♀)	1 ♀

* Study months are not continuous; lone individuals not in groups are also included.

We observed a strong impact of one intense *friaje* on population size in *Saguinus fuscicollis*. We found that 45% of all deaths were caused by the *friaje* of July 2010. Three of the remaining 6 deaths were of males, and three were of older adult individuals, including a presumed death of an older adult male after a particularly severe rainstorm in January 2010.

VII. 3. 4: Group Composition Changes: Dispersal

Emigration events were more common than immigration events for both species (Table VII. 7). Over three years, we assessed a total of 9 possible emigrations (7 were observed) and 3 successful immigrations among *S. fuscicollis* (Table VII. 7). In two years, there were 16 instances of possible emigration (of which 8 were observed) and only 3 successful immigrants among *S. imperator*. Both visits and temporary shifts occurred among *S. imperator*, but only a single visit was seen among *S. fuscicollis*. It was in the context of breeding vacancies created by the severe *friaje* of July 2010.

Table VII. 7: Demographic events across both species during the study period

Demographic Event	*Saguinus fuscicollis*		*Saguinus imperator*	
	# of events	Participant Notes	# of events	Participant Notes
Visitors	1	RIF visited Group SF2 post dispersal from her natal group in July 2010.	2	1 adult male, emigrated successfully into Group SI3 but was then displaced by another male, subsequently seen alone and dispersing; 1 infant female successfully immigrated into SI3, but then disappeared and is presumed dead.
Temporary Shifts	0	No individuals temporarily moved to a new group only to return to their original group and be accepted back.	1	1 infertile young adult female, visited a neighboring group once for *ca*. 3 days.
Immigrants	3	2 adult males, who occupied PBM status in their new group; 1 adult female, who occupied PBF status in her new group, and produced offspring – all assessed post immigration.	3	3 males; 2 adult males successfully emigrated from known groups into new groups and occupied PBM status there; 1 infant male successfully immigrated into SI3 and even mated once with the PBF (unsuccessfully).
Emigrants	7	5 females, none known to successfully join other groups; 1 male, subsequently died alone and without a group.	8	4 of each sex; only 5 successfully visited or immigrated into new groups.
Observed Dispersers	7	Includes all successful emigrants.	7	Includes all successful emigrants but 1 who was not directly observed dispersing.
Possible Dispersers	1	1 infertile female, *ca*. 2 yr old, disappeared and not observed dispersing.	5	4 males and 1 female who could have dispersed to groups outside the study area.

RIF = Roaming Infertile Female; PBM = Primary Breeding Male; PBF = Primary Breeding Female

VII. 3. 4. 1: Gender Effects on Dispersing

Females comprised 88% of all *S. fuscicollis* (7 females of 8 individuals) that likely dispersed during the study, but only 38% were female among *S. imperator* (5 females of 13) (Table. VII. 7). Of observed emigrations, there is a female bias among *S. fuscicollis* (86% of known emigrations), and no gender bias (50%) among *S. imperator*. For every instance of emigration, there are only 0.33 successful immigrants among *S. fuscicollis* and this figure is even lower among *S. imperator* (0.19). Additionally, immigration is biased towards males in both species (100% male in *S. imperator* and 66% male in *S. fuscicollis*) (Table. VII. 7).

VII. 3. 4. 2: Age Effects on Dispersing

One emigrating female *S. fuscicollis* was 30 months old (adult age-class), one emigrating male was an older adult, and neither were successful immigrants. All other known dispersers among *S. fuscicollis*, both emigrants and immigrants, were in the adult age-class. Of the 16 instances of emigration observed in *S. imperator*, we observed 1 infant female visitor (who subsequently died), 1 young adult female who made a temporary shift, and 1 infant male who successfully immigrated; the rest were all adults. The observed successful immigrants were adult males, except for a single infant male.

VII. 3. 4. 3: Breeding Status Effects on Dispersing

Saguinus fuscicollis

Infertile females comprised 67% (N = 6) of all females observed dispersing, and all were likely leaving their natal groups in the 2nd or 3rd year of their lives (Table VII. 8). The remaining two females were seen for the first time while dispersing; they originated from untagged groups outside the study area and appeared to be fertile but nulliparous.

One of the dispersing females from a known natal group was recaptured over the course of the study, and was infertile one month after dispersal, but consistently fertile, nulliparous,

and in a bachelorette group, for up to two years after her first capture. The only male emigrant was an older male capable of breeding but he died within 6 months of assessment, during a dispersal event. Three successful immigrants attained primary breeding status in their new groups, and were only assessed after immigrating into groups; subsequently their breeding status before or during dispersal is unknown (Table VII. 8).

Saguinus imperator

Half the observed dispersers were female (N = 5), and two of them were just short of being considered capable of breeding (vulvar indices slightly < 22 mm), one was a secondary breeding female and one was a nonbreeding infant (Table VII. 8). Three dispersed from identified groups and one was from an unknown group, and none of them were accepted into new groups although a young infant female did visit a group with her twin briefly before passing away. A nonbreeding young adult female made a temporary shift from her natal group to another when she was *ca*. 1.5 yrs old, but returned back to her natal group after a few days.

Table VII. 8: Reproductive characteristics of all emigrants and immigrants in both species.

Species	Individual	Sex	Breeding Status at Time of Capture	Dispersal Status at Time of Capture	IM or EM / Year	Age-class (Months)	Vulva Score/ Index (mm)	Scrotal Score/ Volume (mm^3)	Suprapubic gland score/ Area (mm^2)	Nipple length (mm)/ parity
SFUS	F12	F	IYAd	Pre-D	EM/2011	3	2 / 18.1		4 / 170	0/ No
SFUS	F30	F	IYAd	Pre-D	EM/2010	3	3 / 15.3		4 / 105	0/ No
SFUS	F30	F	RIF	D	EM/2010	3	3 / 14.9		4 / 147	0/ No
SFUS	F30	F	RFF	Post-D	EM/2011	3	4 / 22.8		5 / 335	0/ No
SFUS	F30	F	RFF	Post-D	EM/2012	3?	*		*	*
SFUS	F40	F	IYAd	Pre-D	EM/2010	3	3 / 16.6		4 / 215	0/ No
SFUS	F42	F	IYAd	Pre-D	EM/2010	3	2 / 14.3		3 / 75	0/ No
SFUS	LF1	F	RFF	D	EM/2010	3	4 / 17.4		4 / 303	0/ No
SFUS	LM1	M	BM	Post-D	EM/2009	3		5 / 232	4 / Unk.	
SFUS	F22	F	PBF	Post-D	IM/2011	3	4 / 22.1		5 / 283	4.3/ Yes
SFUS	M12	M	PBM	Post-D	IM/2012	3		3 / 1241	5 / 177	
SFUS	M14	M	PBM	Post-D	IM/2012	3		4 / 1325	4 / 120	
SIMP	M60	M	PBM	Pre-D	EM/2011	3		2 / 759	2 / 123	
SIMP	M60	M	BM	D	IM/2012	3		3 / 711	2 / 160	
SIMP	M61	M	SBM	Pre-D	EM/2011	3		3 / 608	3 / 43	
SIMP	M61	M	BM	D	IM/2012	3		5 / 874	2 / 144	
SIMP	F61	F	SBF	Pre-D	EM/2011	3	4 / 24.7		2 / 133	0/ No
SIMP	F51	F	SBF	D	EM/2011	3	3 / 21.4		2 / 166	3.9/ Yes
SIMP	F51	F	RFF	D	EM/2012	3	3 / 23.3		3 / 169	4.1/ Yes
SIMP	LF1	F	RFF	D	EM/2011	3	2 / 20.5		1 / 0	0/ No

SFUS = *S. fuscicollis*; SIMP = *S. imperator;* Pre-D = Before dispersal; D = During dispersal; Post-D = After Dispersal; EM = Emigrant; IM= Immigrant; Unk. = Unknown or not recorded; Parity = Yes if nipple length > 3 mm (Soini & Cóppula 1981).
IFYAd = Infertile Young Adult; RFF= Roaming Fertile Female; RIF = Roaming Infertile Female; BM = Breeding Male; PBF = Primary Breeding Female; PBM = Primary Breeding Male; SBF = Secondary Breeding Female; SBM = Secondary Breeding Male
* Individual not captured, no measurements available.

Only one of the four observed emigrant males dispersed from a secondary breeding position, subsequently occupying the primary breeding position in his new group. The remaining three emigrant males attempted to shift into a new group when their primary and only breeding female disappeared soon after weaning a pair of infants. Two were originally the primary breeding males in their group, and one was one of the twin offspring. One adult male and the young male infant successfully immigrated into the new group, while the other adult male was displaced and observed to continue to roam without a group (Table VII. 8).

VII. 3. 4. 4: Destinations of Successful Immigrants

Two males moved into the same group of *Saguinus fuscicollis* one year, after the disappearance or likely death of the single resident male. They mated with both breeding females in the group that they joined, and attained primary breeding male status. Another female moved into a group of *S. fuscicollis* that had lost all its females after the *friaje* of July 2010, and she became the primary breeding female in her new group. Unsuccessful immigrants were primarily female and formed bachelorette groups of 2-3 individuals within territories occupied by groups.

Three males moved from Group SI6 into the neighboring Group SI3, which contained two primary breeding males. Group SI3 had recently lost one of its primary breeding males and a secondary male had taken its place. Nevertheless, it accepted the three new males, one only visited, one became a primary breeding male and the last was a nonbreeding infant. One further immigrant moved from Group SI5, where he shared a primary breeding spot with the resident male to another group that contained only a secondary breeding male (i.e. a male with testicular volume indicative of breeding but lower than usual) (Chapter VI).

Female dispersers were also observed roaming together temporarily in bachelorette groups of up to three individuals, as seen in *S. fuscicollis*. However, only one marked group during the full study had a primary breeding female vacancy (Group SI6 mentioned above), and instead of accepting an immigrant the entire group splintered and immigrated into Group SI3.

VII. 3. 4. 5: Causes of Dispersal for Emigrants

Of the known dispersers among *Saguinus fuscicollis,* two young adult females, likely siblings, two years old at the most, were actively chased from their natal group (SF2) by a single young adult female and three males. These chases occurred repeatedly by their natal group, and also by neighboring groups. Another known disperser from Group SF3 (composed of a single PBF, two breeding males, and twin offspring) persists as a dispersing female to this date (see Case 1 below).

Two females dispersed from separate groups and were observed together within the home ranges of three groups. One left a group of two breeding females and males each (Group SI5) and the other left a group with a single breeding female and two males (Group SI3). They were frequently the cause of tense encounters with the resident groups in the area, including their natal groups. The death or disappearance of the primary breeding female in Group SI6 was responsible for the remaining four observed emigration events of the other members of that group (see Case 2 below).

No targeted attacks of the dispersing individuals by individuals in their natal groups were witnessed before they first dispersed, although once the individual made the choice to leave, they were subsequently rarely allowed to return and were chased away (the exception is the single temporary shift witnessed in *S. imperator*).

VII. 3. 5: Risks of Dispersal

Dispersing to a new group is a high-risk behavior in both species, and the following cases illustrate this point for both species.

VII. 3. 5. 1: Case 1 – *Saguinus fuscicollis*

In May 2010, a young female (F30) began separating from her natal group (SF3). In June, she officially dispersed, appearing at a trap-site alone, regularly chased by both her natal group and other tamarins. In late June, a lone female appeared with her, and she behaved aggressively toward this individual several times before slowly accepting her presence. Days later, an immigrant female from Group SF4 joined them in a similar fashion. This bachelorette group of three lived in an area of overlap of at least three groups, two of which were the natal groups of two of the females. After the *friaje* of July 2010, F30's natal group perished, and the bachelorette group disbanded. She then joined Group SF2, which lost both its females in the *friaje*, briefly for a month. Remarkably, this lone female has been seen in 2011, 2012 and 2013, either alone or with other single females in possibly temporary groups, and remains to this day alive and well while still roaming.

VII. 3. 5. 2: Case 2 – *Saguinus imperator*

In 2011, two groups of *S. imperator*, SI3 and SI6, in adjacent territories, consisted of four individuals each, with equal numbers of males and females, but no infants. In 2012, SI6 produced infants but both adult females disappeared. The infants were 7 months old at the time of observation (based on dental data in Chapter IV). SI3 also underwent some changes, now consisting of a single female from the previous year, as well as two males. In late May, a male from SI6 moved into SI3, without any visible difficulties, leaving the infants behind with one male. In July, this male made an unforgettable attempt to enter SI3, dragging with him both the infants. Over two whole days, the existing members of SI3 repeatedly chased the lone male and

the infants multiple times a day, only to have him approach, vocalizing. He made over ten approaches each hour, and by the end of each day, all participants were showing signs of extreme exhaustion, requiring frequent rests on their way to finding a sleeping tree for the night. Finally, three days after the male made his first attempt at joining the group, we observed him mating with the group's female, although still chased for short distances by one of the resident males. Both infant twins began at this time to also roam with this group. The whole experience was dangerous and included increased physical exertion, loud and constant vocalizing, drastic reductions in feeding instances by the group, and several instances of contact aggression. In the end, he was accepted into the group along with the pair of infants from SI6. The female infant did not survive this experience, but the male infant, her sibling, adhered himself to the group's female and even mated with her in one instance, despite his young age.

VI. 3. 6: Breeding Vacancies

We observed primary female breeding vacancies occur due to the death of current breeders in two groups of *Saguinus fuscicollis*, once of unknown causes and the other because of the *friaje* of July 2010. The first vacancy was filled by the second primary breeding female in the group (an unusual case – Group SF1), and the second vacancy by a new immigrant female. Among the males, two primary breeding male positions opened up in 2010 (Group SF1) and two more in 2011 (Group SF1 and Group SF4). The vacancies of 2010 in Group SF1 were not filled in 2011, because a breeding male was still present; however, when he was presumed dead in 2011, two new males immigrated into the group (the duration between these events remains unknown). A secondary breeding male filled the vacancy of 2011 in Group SF4.

All primary breeding females held their positions for two years among groups of *Saguinus imperator*, except in the case of Group SI4 that lost a primary female in 2011, but was replaced by a second primary breeding female. On the other hand, only 5 of the 13 males to ever

hold primary breeding positions in groups retained their position over the course of the two years of study.

VII. 3. 7: Facultative Polyandry

We tested the first prediction of the theory of facultative polyandry and identified all groups with helpers who were at least 1.5 years old, born in the year previous to the one in question (Table VII. 9). We found four cases among *S. fuscicollis* and three among *S. imperator* that fit the requirements. We observed that 1/4 of these groups among *S. fuscicollis* and 2/3 of these groups of *S. imperator* adopted a monogamous mating system with a single breeding pair. However, although they fit the model suggested, none of these monogamous groups reproduced successfully despite having nonbreeding helpers.

Table VII. 9: The evidence for facultative polyandry – groups with helpers born the year before.

Q	Groups with Helpers 1.5 Years Old	SF1	SF4	SF5	SF5	SI2	SI4	SI5
	Year	2011	2012	2011	2012	2012	2012	2012
1	Breeding status of the helpers	NF	SB	SB	NF	NF	NF	NF
2	Were immigrants accepted into breeding positions?	No	No	No	No	No	No	No
3	Were non-fertile group members elevated into breeding positions?	No	Yes	Yes	Yes	Yes	No	No
4	Did the group adopt a monogamous mating system?	Yes	No	No	No	No	Yes	Yes
5	Were there extra males or females in the group?	No	Yes	Yes	Yes	Yes	No	No
6	If yes, what were their fates?	-	Remained	Remained	Remained	Remained	-	-
7	If not monogamy, which mating system did they adopt?	-	Polygynandry	Polygynandry	Polygynandry	Polyandry	-	-
8	Did the group reproduce that year?	No	Yes	Yes	Yes	Yes	No	No

NF = Non-Fertile; SB = Secondary Breeder

A group that conformed to the theory of facultative polyandry should have displayed the following answers to the questions:
Q1 = NF; Q2 = No; Q3 = No; Q4 = Yes; Q5 = No; Q6 = Not applicable; Q7 = Not applicable; Q8 = Yes.

None of the groups highlighted conformed to these requirements, losing out mainly in that they were not reproductively successful.

Table VII. 10: Evidence for facultative polyandry – Groups without non-fertile helpers born the previous year

Q	Groups without Helpers 1.5 Years Old	SF1	SF1	SF2	SF4	SI1	SI3	SI6
	Current Year	2010	2012	2011	2011	2012	2012	2012
1	Mating System in previous year	Unknown	Monogamy	Polygynandry	Polyandry	Monogamy	Polyandry	Polygynandry
2	# breeding males	3	2	2	3	2	3	2
3	# breeding females	2	2	1	1	1	1	1
4	Mating System in current year	Polygynandry	Polygynandry	Polyandry	Polyandry	Polyandry	Polyandry	Polyandry
5	Were immigrants accepted into breeding positions?	No	Yes	No	No	Yes	Yes	No
6	Was the group reproductively active?	Yes	Yes	Yes	Yes	Yes	No	Yes

Facultative polyandry posits that groups without non-fertile helpers (young animals at least 1.5 yr of age) are likely to recruit new helpers through offering mating opportunities in order to reproduce. If this is true, we expect the following answers for the above questions: Q 1 = Any mating system, but ideally monogamy; Q2 = > 1; Q3 = ≥ 1; Q4 = Polyandry or Polygynandry; Q5 = Yes; Q6 = Yes

We found four cases among *S. fuscicollis* and three among *S. imperator* in which groups had no young non-fertile helpers (Table VII. 10). All contained at least one breeding female and two or more breeding males. All cases of *S. imperator* and half those of *S. fuscicollis* displayed polyandrous mating systems, with the remaining two cases of *S. fuscicollis* exhibiting polygynandrous mating. Only one group of each species fit all requirements for Goldizen's model of facultative polyandry, i.e a monogamous group without helpers that accepted immigrants into breeding positions to secure their reproductive output. All remaining groups of *S. fuscicollis* did not recruit new helpers, but were reproductively active given the multiple male and (sometimes) female adults already present in the group. *Saguinus imperator* on the other hand had a group that accepted immigrants and was unsuccessful at reproducing, and one that reproduced without accepting helpers.

VII. 3. 8: Persistence and Lifespans

The mean annual persistence of all individuals in tagged groups of *S. fuscicollis* was 70%, with lower values in 2011 likely due to deaths from the severe *friaje* of June 2010 (2010-2011 April: 57%, 2011-2012 April: 82%). We found an annual persistence for *S. imperator* in 2011-2012 April of 62%.

The mean annual persistence of observed infant *S. fuscicollis* was 72% (2010-2011 April: 60%, 2011-2012 April: 83%), with annual persistence highest in 2012. On the other hand, only 50% of the observed infants born to *S. imperator* in 2011 were alive in 2012. In addition, if *ca.* 80% of all singletons observed were originally one of a pair of twins (Goldizen & Terborgh 1989; Löttker et al. 2004a), the mean annual persistence of infants in either species, mentioned above, would remain approximately the same, since only one instance of singletons was recorded for *S. fuscicollis*.

We observed 3 infant mortalities among *S. fuscicollis*. Two of the infants died immediately after the intense *friaje* of July 2010, while one death has no known cause. The mortalities among infants of *S. imperator* include 2 confirmed deaths, both due to unknown causes.

At this stage in the study, the oldest individual *S. fuscicollis* for whom age could be verified was *ca.* 5 years old, and additional years of study are required for both species to accurately evaluate lifespans.

VII. 4: Discussion

The average group size for this population of *Saguinus fuscicollis* was within reported values for wild groups at other study sites (Goldizen et al. 1996), and does not differ from other tamarin species or genera: *S. geoffroyi* (2 - 9 individuals Díaz-Muñoz 2010), *S. mystax* (Garber et al. 1993; ca. 4-11 individuals Löttker et al. 2004a), and *Leontopithecus rosalia* (2-11 individuals Dietz & Baker 1993). *Saguinus imperator* had a slightly lower group size at this site than *S. fuscicollis*, and appears to aggregate in smaller groups here than do *S. mystax* at other sites (Garber et al. 1993; Löttker et al. 2004a). Further years of data could change these values since *S. imperator* was only observed for 75% of the time spent on *S. fuscicollis*.

Social organization determines group membership and directly impacts possible mating systems by altering the number of breeding individuals available for reproduction (Heymann 2000c). In this study, since all mating events could not be recorded, a mating system was determined based on the number of potential mates available to any given breeding adult in a group, rather than witnessed mating among them. The most common pattern exhibited by *Saguinus fuscicollis* at this site is that of multi-male, multi-female groups, with the potential for any form of mating system to develop within the group. The mating system is subsequently dependent on individual mate choice, existing breeding positions and reproductive suppression (Goldizen 1990; Goldizen et al. 1996; Terborgh & Goldizen 1985). *Saguinus imperator* were

commonly found to exist in single or multi-male groups, with multiple females, making polyandrous mating systems slightly less commonly available as a mating strategy in this species at this site.

Population wide comparisons of the sexes for each species indicate no significant bias towards either sex in any given year. Across the population, from the start to the finish of each field season (~ April to August), we noticed no significant change in either species although annual differences were observed. These ratios appear to be strongly influenced by the number of groups monitored, seasonality, as well as yearly differences in birth ratios, implying that any given year's sex ratios are likely not to represent species-wide trends (Goldizen & Terborgh 1989). Similarly, age-specific sex ratios for both species did not differ significantly from one age-class to the next, and our sample sizes are not large enough to statistically check each class individually for sex biases at this time.

It is more meaningful to examine sex ratios within groups, as both the proportion of adults that are male, as well as direct adult male to adult female ratios. At this site, groups were consistently biased towards males, which is consistent with calculations from studies of *Saguinus mystax* and *S. fuscicollis* in Peru (Goldizen et al. 1996; Löttker et al. 2004a). However, no changes in sex ratio were observed across each field season.

Although overall adult sex ratios do not vary, it is relevant to examine operational sex ratios since they specifically include only individuals capable of mating. We observed many non-breeding females (i.e. females that are not primary or secondary breeders), but very few nonbreeding males in either species. This bias towards males, although influenced by variable factors, has nevertheless been observed across a range of studies on *Saguinus fuscicollis, S. mystax* and *S. oedipus* (Goldizen & Terborgh 1989). A direct consequence of the presence of more males than females within groups is the necessity for males to share breeding opportunities with other males.

Operational sex ratios (Emlen & Oring 1977; Löttker et al. 2004a), or the number of fertile females or primary breeding females available per breeding male in a group, are consistently less than 1, indicating that for both species at this site, polyandry might be the favored mating system (Sussman & Kinzey 1984).

We also observed only *ca* 70% of the animals in studied groups of *S. fuscicollis* persisting from year to year, with even lower numbers among *S. imperator*, signifying a higher turnover rate among the latter. These values are within range of those at both Cocha Cashu with *S. fuscicollis* and northern Peru with *S. mystax* (Goldizen et al. 1996; Löttker et al. 2004a). What then is the fate of the *ca* 30% of the population that does not remain in the study area annually in each species? The two most obvious suspects are mortality and more widespread dispersal, both of which have powerful impacts on individual breeding strategies; while death can give rise to breeding vacancies, dispersal is the primary method of filling them.

The discovery of a dead animal in the rainforest is extremely unlikely, as decomposition is effective and swift in this environment. Therefore, deaths were hard to verify during this study, and many tamarins merely disappeared due to causes unknown. Mortality in both species could be high, but is hard to calculate given the additional possibility that the animal in question could have dispersed to another, unmonitored, territory. Therefore, we posited that age at the time of disappearance would impact the fate of the individual and so, infants and older adults that disappeared were presumed dead, due to high mortalities in these age-categories (25% of deaths were older adults among *S. fuscicollis*) and low likelihoods of dispersal. All other adults and young adults that disappeared were presumed to have attempted to disperse possibly out of the study population. The subsequent disparity in numbers of disappearances observed between the species is likely an offshoot of the exclusion of *S. imperator* from the study in 2010, when the *friaje* of July could have impacted it in ways unknown to us, as well as the generally smaller observation period for this species. This severe

friaje likely caused the deaths of 45% of all missing saddleback tamarins, and along with rainstorms can significantly alter the demography of tamarin populations in this region.

Dispersal events do not always occur at this time at other sites (Goldizen & Terborgh 1989; Löttker et al. 2004a), nor can we be certain that they do not occur the rest of the year when we are not present, but significant changes in group composition have been observed during the dry season, which is also the most likely mating season at this site, since births occur seasonally in the wet season (*cf* Chapter VI). *Saguinus imperator* appears to be more likely to disperse (often repeatednly) than *S. fuscicollis* (lower annual persistence), and this was apparent in the field, with several changes occurring each month of the dry season. A study of *S. mystax* at Padre Isla indicated that *ca*. 14% of the population dispersed in a given year (excluding initial heightened dispersal when groups were introduced onto the island), and in Cocha Cashu, 43% of the original population eventually dispersed (Garber et al. 1993; Goldizen et al. 1996). At this site, we seem to observe the opposite trend, with higher rates of dispersal among *S. imperator*, a close relative of *S. mystax*, than among *S. fuscicollis* despite side effects of a severe *friaje*.

Overall, there are fewer successful immigration events than there are emigration events, implying that dispersal is a risky behavior that does not always succeed and could end in death. There was a bias towards female dispersers among *S. fuscicollis*, and the opposite trend among *S. imperator*. There is a large difference between the success rates of males and females, however, with more male dispersers successfully entering groups to acquire breeding positions than females, across both species. In the case of *S. imperator*, there is a preponderance of successful male immigration events, which is consistent with other sites (Löttker et al. 2004a), but these events are fraught with high-risk behaviors (increased vocalization, reduced feeding, heightened visibility to predators) for both the individual and the group. Among *S. fuscicollis,* females tend to disperse more than males, which is again consistent with data from Cocha Cashu (Goldizen et al. 1996).

VII. 4. 1: Breeding Vacancies and Success

The breeding success of an individual is dependent on both its physiological makeup and breeding position openings within a group (Garber et al. 1993; Goldizen et al. 1996; Goldizen & Terborgh 1989; Terborgh & Goldizen 1985). At this site, we observed a few cases of multiple primary breeding females in groups, but a single female monopolized breeding in most groups. This is supported at other sites (Goldizen et al. 1996; Terborgh & Goldizen 1985), and at CICRA, the entry of dispersers of either sex is not tolerated well. We observed several agonistic interactions involving prolonged chases and lunges, and a tendency for dispersers to travel lower in the canopy to avoid other tamarin groups in the area. Further, we frequently observed lone dispersers and dispersers in small single-sex groups in association with established groups of the other tamarin species.

Given that breeding vacancies must exist for a new female to begin breeding in most groups, stochastic events within a population that remove or displace breeding individuals have an especially significant impact on every aspirant. This was never more evident than in the aftermath of a severe *friaje*, or cold-front, in July of 2010. This single event, spanning almost 7 days of extremely low temperatures, was responsible for 45% of all deaths confirmed among *S. fuscicollis* that year. Although *S. imperator* was not included in this study that year, and given the similarities between their ecological niches, there is no reason to doubt that they experienced similar strains as well. This is particularly relevant for females, due to restricted breeding opportunities (Goldizen et al. 1996) and long tenures of primary breeding females (Garber et al. 1993; Löttker et al. 2004a). Supernumerary males are tolerated among groups, mating is shared, often amicably, making breeding vacancies likely less critical to male reproductive success.

We also noticed that breeding male positions were often created anew, without the removal of the existent male, while this was never the case among the females. Most

interestingly, primary breeding females appear to cement groups together among *S. imperator* as evidenced by two factors: 1) all but one primary breeding female held their breeding positions during both years of the study and 2) when one primary female disappeared, her group immediately splintered and emigrated to a neighboring group. Even when primary breeding vacancies originated, often females within groups took up these positions, and this behavior is not complemented by the acceptance of young females into the same group subsequently.

This suggests a harsher climate for females in both species, where competition is high not only for breeding but also for group membership of any kind, as confirmed by extremely low immigration rates over thirteen years at Cocha Cashu with *S. fuscicollis* (Goldizen et al. 1996; Goldizen & Terborgh 1989; Terborgh & Goldizen 1985). Our data also confirm that young female *S. fuscicollis* with less than average adult values for reproductive characteristics are likely to disperse, and on occasion, older males are also displaced from their groups. One female has been alone and dispersing for three years to date, which has never been reported before, and is only observable at this site due to our consistent ability to identify individuals. Female *S. imperator* are mostly reproductively mature at the time of dispersal, and very rarely, a younger female will attempt to disperse as well. Further, in this study we have never observed a lone older female survive without a group to date. Older males seem not to suffer the same consequences, and are observed in groups despite possessing depressed testicular volumes that could imply cessation of meaningful reproductive activity.

VII. 4. 2: Facultative Polyandry

The theory of facultative polyandry has received much support since it was put forth based on data on *S. fuscicollis* at Cocha Cashu (Goldizen 1987a; Goldizen 1987b). Although it is based on several pieces of concrete evidence, such as the lack of reproduction among monogamous pairs without one or more helpers, and the contribution of nonbreeding (or

nonfertile) individuals to alloparenting, it appears that data from our study do not support the predictions of the theory as strongly as expected.

In the case of lone breeding pairs with one or more nonbreeding helpers (typically infants from a previous year), the theory predicts that no recruitment of additional helpers is necessary for the successful raising of offspring (Goldizen 1987b). Given 15 group-years of study for *S. fuscicollis* at this time, and 12 group years for *S. imperator*, we were unable to locate a single group that adopted this strategy with success (although some attempted it but never raised infants to 4 – 6 mo of age). In the second case of those groups without young helpers, the theory predicted that new helpers would be recruited and mating opportunities shared with them to secure their assistance in the rearing of future young (Goldizen 1990). Only one group of each species fit these criteria, and reproduced successfully; however, many others already possessed helpers, which did not guarantee the successful rearing of offspring. While this theory appears to explain the possible options for lone breeding pairs, it is likely that the predominantly multi-individual group composition observed at this site makes such strategies less relevant.

In the next few years we will have the opportunity to gather information on several significant landmarks in the reproductive lifespan of an animal. We currently have several females in each species poised to either begin reproducing in their natal groups or outside them, depending on whether they chose to stay or disperse to gain a breeding opportunity. We will be able to distinguish between these two strategies and evaluate the reproductive output of each to identify the more successful one for each sex in each species.

VII. 5: Chapter Summary

1. Groups of both *Saguinus fuscicollis* and *S. imperator* commonly include multiple males and females, providing opportunities for polyandrous, polygynous, or polygynandrous mating systems.
2. No sex biases of group, or overall, sex ratios were observed in either species, and no significant differences in sex ratios were observed between the beginning and end of the field season (*ca.* April to August).
3. Environmental events with cyclical and stochastic components, such as *friajes,* can produce a strong impact on mortality rates among these populations, which in turn open up breeding vacancies within groups.
4. Immigration events are rare and highly dependent on available breeding vacancies among females, but males do enter groups with other breeding males present.
5. The primary emigrants among *Saguinus fuscicollis* are females, while those among *Saguinus imperator* are more male-biased.
6. Facultative polyandry could be a possible mating strategy for a lone pair of breeders, but most groups already contain multiple breeding individuals of each sex and among them, morphological characteristics and demographic variables interact to determine individual mating and breeding success.

Chapter VIII: Summary and Conclusions

The goal of the present study was to examine the reproductive complex in callitrichids – habitual twinning, cooperative polyandry, and genetic chimerism – in the context of future genetic studies, on two sympatric species of callitrichids in the wild. I attempted to achieve three specific goals – first, to examine the morphological variation between two sympatric callitrichid species, as a natural experiment with relatively similar habitat and methodology for both species; second, to evaluate the age and reproductive status accurately for all individuals, including those that might be reproductively suppressed; and third, to compare the group compositions, mating systems and dispersal patterns of both species to evaluate the influence of cooperative polyandry on reproductive success. It is critical to document group structure and membership, as well as individual dispersal, reproductive success, and the development of offspring across callitrichid species, in order to better understand the evolutionary advantages of this unique system of reproduction.

In order to achieve these goals, I habituated a population of two callitrichid species to observation, the saddleback tamarin (*Saguinus fuscicollis*) and emperor tamarin (*Saguinus imperator*) in southeastern Perú. I then worked with several groups of both species to collect measures of their morphology, dental casts, and body weights, while placing identification tags on each individual. Every year, from 2010-2012, I re-assessed the callitrichids working for three years with the saddleback tamarins, and for two years with the emperor tamarins. The study site (CICRA) is located in the Madre de Díos Department of Perú, and twenty-five years ago, a gold mining company owned the land and the wildlife was subject to poaching. Therefore, the large-bodied spider and howler monkeys are present at lower densities than expected, which might account for the relatively high densities of small and medium-sized primates at this site, including the callitrichids.

At the end of the three years, I was able to provide a detailed description of both primate species and their reproductive morphology and behaviors. Although genetic data were collected at this site, they have not been analyzed at this time, as this work is pending permits from the Peruvian government. Nevertheless, the picture I can paint of these two species, co-existing within the same environment, is broader in its scope than most other long-term work on callitrichids in the wild.

VIII. 1. The Saddleback Tamarin at CICRA

The saddleback tamarin weighs *ca*. 350 g, has dark pelage, shows no sexual dimorphism in size, and no sex differences in appearance. It experiences a short but successful infant life-stage, with a high probability of surviving to adulthood, in which they remain and reproduce for several years. When their teeth degrade to the extent of appearing almost completely flat, they do not survive longer than a year, but continue to successfully reproduce right up to their demise (Chapter IV).

This species exhibited seasonal birth patterns, with both singletons and twins observed at this site (Chapter VI). Unlike previous work that determined specific thresholds for reproductive values beyond which individuals could be considered sexually mature adults (Soini & Cóppula 1981), I found a range of variation among juveniles and adults in this species, and such thresholds (if any) were quite different than those predicted for the same species at a different site. This suggests that some of the variation observed could be reflective of population-level differences, likely due to extended isolation from each other over time.

Saddleback tamarins tended to have groups that contained adults of both sexes, with only a few examples of male or female dominated groups (Chapter VI). There was no remarkable difference between the proportion of adult males and females in the population, groups, or age-classes (Chapter IV). However, there was a tendency for the infant and young adult classes to be more female biased than the adult and older adult classes, indicating a slight

attrition of females, as they age through their different life stages. This suggested to me that any possible mating system could develop within these groups – monogamy (a single breeding pair), polygyny (multiple females breeding with a single male), polyandry (multiple males breeding with a single female), or polygynandry (multiple mates for individuals of both sexes) – and they do (Chapter VI).

Since recording every fleeting mating event for all adults in the population was beyond the scope of reality, I assessed potential mating systems by the number of individuals in a group of that were capable of breeding. In this species, groups of just one adult breeding male and female were rare, and did not reliably reproduce success fully (Section VI. 3. 7). Most groups either contained one breeding female and several breeding males, or contained multiple breeding females and males. As has been alleged of other callitrichids (Sussman & Kinzey 1984), males appear to be central to ensuring the survival of offspring, with at least two males per successful group (Chapter VI). However, this did not necessarily mean single dominant breeding females in groups, with several instances of stable groups with multiple primary breeding females in them. Therefore, although I did observe signs of reproductive suppression (i.e. three years before any female acquire secondary breeding status, or lower vulvar indices and suprapubic gland areas in secondary breeding females), it appears that such suppression is not maintained strictly throughout the lives of these females (Chapter VI). In one case, I even recorded single surviving infants that were a few months apart in age born to two separate females in the same group.

Instances of multiple breeding are certainly not the norm among callitrichids, as reviewed by Smith et al. (2001). This fascinating flexibility in reproductive systems of saddleback tamarins reveals that their breeding system at this site cannot be subject to simple categorization. Although they do not adopt the strictly monogamous relationship that they thrive in when in captivity, they do not appear to be strictly polyandrous either. Thus, viewing

callitrichids through the lens of a single mating system might be misleading, and certainly not completely accurate for this species.

Saddleback tamarins have stable adult life stages, with an estimated maximum lifespan of 10-15 years, which is supported by evidence from other study sites (Goldizen et al. 1996; Löttker et al. 2004a). Over two-thirds of their population survives annually each year at this site, but this figure is subject to change primarily by acute weather events. At this site, the population appears to be expanding slightly, with a pattern of distribution of individuals across age-classes (infant, young adult, adult, or older adult) that is in agreement with that of other viable primate populations (Chapter IV). Overall, there appear to be no threats to the stability of this species at this site, and in fact, densities here are higher than reported at Cocha Cashu, a biological field station within receiving governmental protection within Manu National Park (Table I.1). This is most likely due to the higher densities of larger-bodied primates at the protected site of Cocha Cashu, that are still recovering from previous hunting pressures at CICRA, to the advantage of the smaller-bodied callitrichids at this site. Despite this site including secondary forests, or selectively logged woodland forests, it is an important location that sustains an expanding population of this species, and its future protection is strongly recommended.

VIII. 2. The Emperor Tamarin at CICRA

The emperor tamarin is morphologically distinct from its counterpart, the saddleback tamarin, both in general pelage (which is grey), and in an elaborate display of facial morphology. Both males and females possess a white mustache and beard that develop quickly in their first year. They are not sexually dimorphic. They are considerably larger than the saddleback tamarins, with an average weight of *ca*. 600 g. This study revealed that the extra mass does not create an overall increase in size (or body/limb length), but instead, is manifested in thicker limbs.

Their rugged appearance in comparison to the saddleback tamarins mirrors their general demeanor – they demonstrate behavioral dominance over saddleback tamarins. Although in some populations, sympatric callitrichids that form polyspecific associations have been seen to stratify the canopy while roaming together, observational evidence for such stratification is lacking between the species at this site. This could be due to their more dominant behavior, as well as their general lack of niche specialization (Buchanan-Smith 1999), as compared to the red-chested tamarins, for example, that form polyspecific associations with saddleback tamarins where they are syntopic (Rehg 2006).

Emperor tamarins experience a stable infant stage, followed by a young adult stage that some animals do not survive, but during which some not only survive, but also reproduce. They then enter an adult stage that extends for a shorter period than the adult phase in saddleback tamarins, based on data on several seasons reported here. Once they move into the older adult phase, however, despite it extending for as long as 2 years in some cases, they do not reproduce any further. Their life histories, therefore, are not identical to that of the saddleback tamarin, although both species agree in general with the average primate life history. Further study is certainly necessary to confirm this pattern among emperor tamarins, since so little is known of them in the wild.

The emperor tamarins are not reproducing as quickly or successfully as are the saddleback tamarins at this site, but when they do, they tend to raise both infants successfully and single infants were never observed. Due to the lack of long-term studies of this species in the wild, no comparative sample exists with which to compare the range of variation in reproductive behaviors observed here. Some comparisons to saddleback tamarins and mustached tamarins at other sites can nevertheless be drawn.

Emperor tamarins were predominantly found in groups with more adult males than females, with some mixed-sex groups. This implies that, other than polygyny, any mating

system could develop within these groups. Like the saddleback tamarins, the emperor tamarins did not display skewed sex ratios. Further, the tendency for the infant and young adult classes to be more female biased than the adult and older adult classes was less evident in this species. This indicates that an attrition of females in this species is not as pronounced as with the saddleback tamarins at this site. This has importance for sex-biased dispersal, which is a major cause for animal disappearances.

Mating systems, which reflect the numbers of breeding individuals of each sex in a group, rarely were monogamous and when so, reproductively unsuccessful (Section VI. 3. 7). Despite the ability to form some polygynandrous groups, most emperor tamarin groups were markedly polyandrous. Every group that raised infants to at least 4-6 months of age contained at least two breeding males, confirming that emperor tamarins follow a more typical callitrichid model of cooperative polyandry at this site.

This was accompanied by almost a complete lack of multiple breeding females in the same group, save for one instance. This implies that reproductive suppression is stricter in emperor tamarins, or that dominant breeding females are intolerant of other females in their groups entirely. There are several females poised at the cusp of their third years that will make the choice to either remain or disperse in 2013. If they stay, it will be fascinating to examine if they coexist with their mothers for breeding positions, or if they will be forced to leave the group or displace the dominant female entirely. Male reproductive suppression was also displayed; with a distinctly low testicular volume group of males, which brings into question the future of male offspring in their natal groups. Further study will be illuminating in this regard.

Finally, assessments of lifespan in the emperor tamarin indicate that they too have stable adult life stages, with maximum lifespans estimated to be 7-10 years. This is a value that is noticeably lower than that of saddleback tamarins, for which the primary explanation is likely an undersampling of this population at this time. It could be that the dental rate of wear is slower

than that of the saddleback tamarins, due to differences in feeding ecology or microhabitats, which could increase my estimates of their lifespans. While these possibilities exist, I believe that they are best evaluated after further sampling of this population, in order to eliminate a nonrepresentative sampling method as a possible cause for these differences. While it is likely that emperor tamarins are successful and thriving at this site, further evaluation is necessary to confirm that this is true, at least to the extent to which we are confident of these estimates for the saddleback tamarins at this site.

VIII. 3. A Broader Picture of Cooperative Breeding

Saddleback tamarins are taxonomically distinct from emperor tamarins, belonging to the hairy-faced group of tamarins rather than the mustached tamarins. Therefore, by assessing these two relatively distantly related callitrichid species within the same habitat, alongside the same methodology over a fixed time period, a natural experiment is created, and those characteristics that are constrained by ecology could be distinguished from those specific to a species. Similarities between the two species could be explained by a shared habitat in some cases; on the other hand, differences between them in any regard could be due to their differing taxonomic histories, since their environment is relatively similar and their ecology could be expected to follow suit.

VIII. 3. 1. The Influence of Environment on Species-Specific Traits:

Despite differing reproductive morphology and behaviors, as described above, twinning and strong birth seasonality were observed in both species, which is consistent with other sites (Garber et al. 1993; Goldizen et al. 1996; Löttker et al. 2004a; Savage et al. 1997; Soini & Cóppula 1981). Both tamarin species experience breeding seasons that overlap almost entirely, with a slightly broader season among saddleback tamarins than emperor tamarins. Most significantly, no births were not observed in either species, from April to August each year, which coincides with the dry season and low fruit availability. Mustached tamarins give birth

nine months of the year in northeastern Perú (Löttker et al. 2004a), and year round at Padre Isla (Garber et al. 1993), which is in marked contrast to emperor tamarins at CICRA, despite their closely relatedness. This reflects the sizeable influence of the environment on birth timings, which has a similar influence on both species at this site. It would be very interesting to confirm if the slight delay observed in the emperor tamarin birth season at CICRA, persists at Cocha Cashu, as that would support the idea that even microhabitat differences in local weather patterns can alter breeding seasons within the same species at two neighboring sites.

Molar occlusal wear can be strongly influenced by dietary differences between species, which in turn are reflective of site-dependent feeding ecology. At Padre Isla in Perú, an assessment of age based on dentition of mustached tamarins relied heavily on regular wear of incisors and canines with age (Garber et al. 1993). At CICRA, however, canine wear did not reliably increase with molar occlusal wear, which implies that specific site differences between Padre Isla and CICRA, reflecting different food resources, can strongly affect dental wear between sites. Given this and preliminary data that indicates that the saddleback and emperor tamarins share many of the same resources at this site, I believe that it is likely that their shared habitat and feeding ecology reflects a similar rate of wear on their teeth. Therefore, the use of the same grading system for tooth wear in both species is justified.

VIII. 3. 2. The Influence of Taxonomy on Species Specific Traits

Female scent glands are larger than those of males in both species at this site, which is supported across other species within the genus *Saguinus* (Garber et al. 1996; Soini & Cóppula 1981; Zeller et al. 1988). This suggests several intriguing possibilities, one of which is that competition for males is high, requiring females to advertise their reproductive status to secure breeding. This would be unlikely if polyandry was common, and males were easily available in the population to a breeding female. My study indicates that emperor tamarins adopt polyandry more readily than do saddleback tamarins, encouraging, which leads me to predict that female

saddleback tamarins likely scent-mark more frequently than do female emperor tamarins. Studies from northeastern Perú indicate that mustached tamarins (close relatives of emperor tamarins) scent-mark less frequently than do saddleback tamarins (Heymann 2001), but this remains to be tested at CICRA with emperor tamarins. Further, an evaluation across New World primates that scent-mark indicates that the primary purpose of scent-marking is for intrasexual competition and intersexual mate choice (Heymann 2006). This suggests that scent-gland morphology is not subject to ecological influence, but instead is species-specific and taxonomic differences can be expected between the two species in functionality and morphology.

However, some captive studies have indicated that callitrichids that are spayed or neutered early in life will not develop functional suprapubic scent glands, while even a delay of a few months in performing gonadectomies can avoid affecting scent development (Epple 1982; Epple 1981). This suggests that scent-marks may indicate more than reproductive status across both species, if only to a certain extent. In fact, a recent evaluation of the patterns of scent-marking across home-ranges among saddleback tamarins in northeastern Perú revealed that tamarins do not mark strictly along core or peripheral areas of their territories, but instead at feeding trees commonly used by multiple groups (Lledo-Ferrer et al. 2011). It appears that they deposit marks where other groups are likely to find them, and thus share information about themselves with their neighbors. This could be in the form of reproductive statuses, but also such fundamental information such as number of individuals, sex, as well as importance of an area to the group. Information on scent-marking behaviors will be collected and analyzed at this site to evaluate these possibilities, while considering possible interspecies communications also.

Both species show evidence of reproductive suppression – among the females this is in the form of delayed reproduction and in the males, it could possibly result in reduced testicular volumes, which in turn could indicate lower reproductive success. An evaluation of endocrine profiles for both sexes as well as genetic data on paternity will allow me to clarify the question of

reduced testicular volume in males. Overall, however, reproductive morphology does not appear to be an accurate indicator of age. I observed differing schedules of maturation between males and females as well, for both species, which introduces more error into morphology-based age-determinations. Reproductive morphology proved to be an excellent way to distinguish infants from other individuals, but the large range of variation observed among the other individuals did not allow me to tell the other age-classes apart. These data highlight once more the importance of evaluating age among callitrichids based on dental information, given that reproductive suppression can cause an individual callitrichid to appear younger than they actually are.

Reproductive suppression could be effective to varying extents in either species at this site (to be evaluated in the future). Given that dominant females have a choice in terms of how tolerant they are of other females in a group, with more tolerance displayed by saddleback tamarins than emperor tamarins at this site, it is possible that there is a higher level of competition for territories among emperor tamarin groups and thus, less flexible mating systems in general. I could evaluate this by examining both home-range sizes as well as group stability over time in both species. If the saddleback tamarins exhibit more fluid groups and home ranges, with higher likelihoods of formation of new groups over time, while emperor tamarins remain primarily in stable groups with single dominant breeding females and inflexible or larger home ranges, then this assumption would be supported. Given relatively similar feeding ecologies within identical habitats (emperor and saddleback tamarin home ranges overlap entirely), this could also imply a lack of ecological influence on reproductive suppression, and instead, a species-specific physiological adaptation.

In both species at this site over the study period, emigration events are more common than are immigrations, and the latter are biased towards males. If this were a closed population, one could assume then that as individuals disperse, a majority are unsuccessful and die.

However, surrounding the study site is more viable habitat filled with further groups of tamarins, and callitrichids are known to disperse as far as two groups away (Goldizen et al. 1996; Löttker et al. 2004a). Therefore, there is a possibility that individuals that disappear from this population are emigrating outside of our study area. Nevertheless, if the intrinsic rate of successful immigration into groups is comparable to that of successful emigrations out of groups, then it logically follows that individuals from outside the study area should also disperse into our focal groups. This assumes that human observers do not bias outside individuals against the groups, and given that observation is largely present for only three months annually, and most dispersal events occur outside of those time periods, we do not expect this assumption to be violated. However, this is not occurring at this site, and thus the disparity between emigration and immigration is likely a consequence of natural attrition of young adult individuals at this site during risky dispersals with low success rates. This brings into question the relevance to survivorship of risks associated with dispersal for both sexes.

Interestingly, among saddleback tamarins at least, we have observed on several occasions, bachelorette groups of lone dispersed females that roam together. In one case, one such female has been with a variety of other lone females for three years and counting. These individuals do not emit contact calls frequently since they often share overlapping home ranges with other larger groups, and are at a severe disadvantage during intergroup encounters. Thus it is possible for lone individuals to survive without mates under the radar, and it is likely that these individuals are often ignored during censuses. The male biased immigration observed at this site could be a consequence of reduced sampling, since dispersal is a rare event compared to other behaviors. Information from Cocha Cashu nearby indicates that males and females disperse among saddleback tamarins (Goldizen et al. 1996), and further sampling at CICRA could confirm this to be true at this site as well. However, during my study there were several months of the year during which observers were not present at the site, during which several dispersal events could have occurred in one or more directions that could not be evaluated in

this study. While the ecology of the site could influence the timing of dispersal (i.e. resource availability and mating seasonality could influence decisions to disperse), it appears that the number of animals that disperse of each sex in either species is likely a consequence of more ingrained, species-specific, group structures.

At this site, I also observed less of an attrition of female emperor tamarins across age-classes, than female saddleback tamarins. This could imply either that fewer females were born or that females were dispersing less often and remaining in their natal groups. We know that females often disperse however, implying that a sex bias in birth statistics is more likely. Interestingly, we do observe slightly higher numbers of female infants than male infants in both populations; however, these are not birth statistics and only reflect those that survive to 4-6 months of age. One could argue that in this case, these numbers have an advantage over true birth statistics, as they incorporate survivorship of infants as well. Further, to be perfectly certain of this bias, we need to examine a third year of data for the emperor tamarins. This is because that is the year during which the saddleback females made a decision to stay or disperse, and this would be critical to understanding the sex bias in dispersal for both species.

VII. 4. Acute Weather Phenomena

In July of 2010, there occurred a severe storm, a cold front of wind that swept up over the Patagonian plains to the foot of the Andes where CICRA lies. Temperatures dropped from 24 to as low as 7°C, and this lasted 39 days of which at least 16 were below 15°C. Animals began to die after the first week, and could be found scattered across trails, perfectly preserved for it was too cold for even the most efficient forces of decomposition typical of tropical rainforests. During that year, this project monitored saddleback tamarin numbers across several groups. In 2011, when I returned to conduct a census of previously identified individuals, I found that only 57% of all those present in 2010 were alive in 2011. In 2011 I censused only 14 saddleback tamarins (from *ca*. 25 the previous year), which included new individuals born into the

population as well as a couple of new immigrants. Remarkably, 2011 made the first census for emperor tamarins, and I assessed over 25 individuals, comparable to pre-friaje numbers for saddleback tamarins in 2010. How was it that the emperor tamarin population had not been affected by this event? One explanation was that they were generally higher in density to begin with, something that we know not to be true given two yearly censuses at this time. Could it be that the emperor tamarins were simply better equipped for such phenomena? Given that these two species have lived sympatrically within the same habitat, why would only one of them evolve such an adaptation? I believe that the answer lies in their body weights – an individual emperor tamarin, without increasing its size, has a higher body mass. It achieves this by bulking up its limbs and overall girth, which could assist in thermoregulation by reducing overall heat loss. Either way, it is certainly interesting that a more cold-adapted species in the Amazon basin is likelier to survive than those adapted for the most common weather pattern year-round – that of sweltering heat and humidity.

During the *friaje*, group SF2 (saddleback tamarin) completely vanished. We found at least one carcass beneath a sleeping tree, and no other evidence for the group ever surfaced. A combination of the cold front, as well as a hungry predator might explain their demise. I expected that the effect of this suddenly empty territory in the very center of the study area, surrounded as it was by other groups, would not last more than a few days without tamarins moving in to occupy the now empty territory. As it was, there were several groups of lone females dispersing through the area, which at the very least ought to have been interested in a new home. Fascinatingly, this never occurred. In fact, even after a year, we noticed that the surrounding groups gradually expanded their own home ranges to overlap more with the missing group's territory, but they never fully took it over and no new group formed in its stead. Such acute weather phenomena at CICRA are not aberrations. An analysis of weather patterns since 2000 revealed at least one event that was even more severe, with several that were only slightly less severe occurring during the dry season (or winter) each year (Chapter I). Further,

this particular event opened up several breeding positions for both males and females, which were filled almost immediately after the event by individuals from outside the study population. It appears therefore that breeding positions are in high demand, with several contenders for new such positions, while home ranges themselves are likely rarely evacuated, without any familiar mechanism in existence for filling them.

VIII. 5. Ideal Breeding Conditions for Callitrichids at CICRA

Reproductive success is a means to evaluate the overall success of a breeding strategy adopted by a group in any given year. I found that monogamous pairs very rarely were able to successfully raise infants to 4-6 months of age, while virtually all groups with successful twin offspring contained at least two males in both species. While no single infants were ever observed with emperor tamarins, we did find singletons among the saddleback tamarin offspring. These factors suggest that both species adopt slightly different means to achieving maximum reproductive output, if indeed that could be assumed to be their overarching goal. We know that overall mean rates of reproductive success per group are higher by almost a third among saddleback tamarins.

The saddleback tamarin appears to be a species with loosely enforced reproductive suppression, resulting in the presence of multiple (sometimes successfully) breeding females in a group. In several of these cases, only single sets of offspring survived, but since I conducted censuses when these offspring were 4-6 months old, after the usual age at which they were weaned, I occasionally had to predict the most likely mother for the infants in a group based on reproductive morphology. While it is quite likely that both infants belonged to a single female, the presence of a second female of primary breeding status suggests that it is possible, if not probable, that both females could have given birth in the same month, either to a single infant each or to twin pairs that had subsequently lost an infant. Overlaying genetic data from these individuals to determine parentage will elucidate these issues efficiently; at this time, however,

in the absence of these data, this suggests that saddleback tamarins have acquired a higher reproductive output than emperor tamarins without resorting to exclusive cooperative polyandry. Although additional males appear necessary for the successful rearing of offspring in this species, when these males are present, multiple breeding females can be sustained within the same group.

Among emperor tamarins, a more strictly polyandrous mating system appears to be the rule. However, in several years in this species, groups entirely fail to either produce offspring or raise them to post-weaning ages, and this is far more common in this species than among the saddleback tamarins. When they do raise infants, however, they do so with a high rate of success, since single offspring where never observed at this site. As conditions for maximum reproductive output go, it appears that a more loosely suppressed mating system for females in conjunction with multiple males produces a higher reproductive output over time. This implies that we are likely to see more stable extended family groups among emperor tamarins than we are among saddleback tamarins, where emperor tamarin siblings tend to share the same mother and father, while saddleback tamarin siblings might only share one parent. Cases of male siblings transferring into groups as a pair have been noticed in the wild (Garber et al. 1993; Goldizen et al. 1996; Löttker et al. 2004a), implying that sibling bonds are important and sometimes long-lasting in these species. At CICRA, based on the information recorded thus far on both species, it appears that saddleback tamarin siblings might be less related than are emperor tamarin siblings, which in turn could have possible ramifications for future affiliations.

One major difference between the two species was the lack of differentiation between male and female suprapubic glands among emperor tamarins, and indeed, the general lack of development of these glands across the species itself (Table V. 4). Some explanations are possible for this distinction. First, they possess another scent gland located over the sternum that is virtually absent in, and certainly almost never used by, saddleback tamarins. This gland,

although present, is so small and covered with hair that it is hard to assess in terms of size or development, and further observation is necessary to determine exactly how functional it is in comparison with their suprapubic gland. Second it is possible that the external appearance of a gland does not directly relate to the internal structure or functionality of the gland as a whole (Zeller et al. 1988), which could in turn explain the lack of correlation between the slightly diffuse glands in male emperor tamarins and their testicular development. A future evaluation of scent marking behaviors between the species could provide great insight, and is being undertaken at this site. If females mark more than males, this would imply that increases in gland sizes could reflect increased functionality and dependence on the gland itself during scent deposition. If general differences in frequencies of scent marking exist between the species, despite similar glandular areas within each sex of a species, this would indicate that gland sizes in one species could not be compared to those of another species of callitrichid, likely due to differing internal morphology and behavioral functionality.

Overall, this study elaborates on a single, yet important, point – callitrichids, despite their history of being assigned strict breeding systems, are likely extremely flexible in this regard. While they maintain group membership with much exclusivity, making it difficult for dispersing individuals to gain access into groups, there appears to be variation between species and between groups of a species in the mating system they adopt. Their singular suite of reproductive characteristics – habitual twinning, cooperative breeding, and genetic chimerism – might be best viewed through the lens of a mating system that adapts to changing social situations to achieve reproductive outputs that maintain overall population stability. Further study over multiple years is required to effectively describe their breeding systems in the context of genetic relatedness and chimerism, and is currently being undertaken at this site.

IX. Bibliography

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